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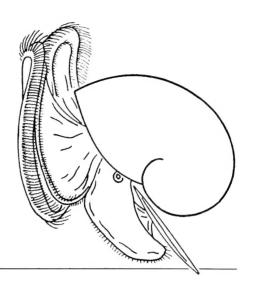# AUTHOR INDEX

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The Functional Morphology of the Pedal Musculature
of the Marine Gastropods *Busycon contrarium* and
Haliotis kamtschatkana

by

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Abstract. The gastropod foot shows a high degree of morphological complexity and behavioral plasticity. This study describes the arrangement of the muscle fibers and connective tissue in the feet of *Busycon contrarium* and *Haliotis kamtschatkana* and analyzes the functional roles of the various muscle groups in wave propagation and other pedal actions. In addition, it presents the role of the connective tissue as an essential element in pedal function. The prosobranch foot is primarily solid muscle: it consists of two structurally and functionally distinct regions, the columellar muscle and the tarsos. The region of the columellar muscle consists of thick bundles of muscle fibers wrapped in connective-tissue sheaths and arranged in an orthogonal latticework. The muscle fibers of this region perform the gross shell-foot movements: protrusion, retraction, shell elevation, and twisting. The tarsos also consists of bundles of muscle fibers wrapped in connective-tissue sheaths. In this region, however, large bundles from the dorsal portion of the region divide into finer and finer branches as they approach the sole and sides of the foot, forming a network of small groups of muscle fibers embedded in a dense connective-tissue matrix. This muscle system is responsible for the finer movements of the foot, including propagation of locomotor waves, manipulation of prey, and formation of egg capsules. In both regions, the connective tissue, by transmitting compressive and tensile forces, probably provides the mechanism by which one set of muscle fibers can directly antagonize another.

INTRODUCTION

The gastropod foot is a fleshy, flexible organ that performs a diversity of functions. Besides locomotion and adhesion, a snail can also use its foot to capture and consume prey, to mate, to shape and deposit egg capsules, to clean its shell, and to thwart potential predators.

Although the external characteristics of the gastropod foot have been thoroughly described and classified (VLÈS, 1907; MILLER, 1974a, b; GAINEY, 1976) there are relatively few studies of the internal organization, and even fewer that relate structure to function: TRAPPMANN (1916) described the arrangement of the musculature of *Helix pomatia* Linné; ROTARIDES (1941, 1945) described the organization of the musculature of *Nassarius mutabilis* (Linné) (=*Nassa mutabilis*) and of several limpetlike forms; JONES & TRUEMAN (1970) described the pedal musculature of

Patella vulgata Linné, 1758; JONES (1973) described *Agriolimax reticulatus* (=*Deroceras reticulatum* (Müller)); PLESCH et al. (1975) described the body wall and pedal musculature of *Lymnaea stagnalis* Linné; GAINEY (1976) described the pedal musculature of *Neritina reclivata* (Say, 1822) and *Thais rustica* (Lamarck, 1822); and TRUEMAN & BROWN (1976, 1985, 1987) described the pedal musculature of *Bullia digitalis* (Dillwyn) and *Haliotis midae* Linné. In most cases, however, the authors were primarily interested in identifying muscle systems and in describing the orientations of the muscle fibers within the foot.

The complicated patterns of muscular organization in the gastropod foot have prompted workers to propose several possible antagonists for the muscular contractions of pedal waves. JORDAN (1901, 1905) believed that the pressure of the blood in the lacunae extends the relaxed muscle in the foot of *Aplysia limacina*. TRAPPMANN (1916) suggested that the transverse muscle fibers provide the necessary antagonistic force in *Helix pomatia*. SIMROTH (1878) proposed that the muscle fibers involved in locomotion actively expand, as well as contract. Separate explanations

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have been proposed for the mechanisms of direct and retrograde wave propagation and for burrowing (see TRUEMAN [1983] for review).

A hydrostatic skeleton is any "fluid mechanism which in one way or another provides a means by which contractile elements can be antagonized" (CHAPMAN, 1958). Because the only requirements are that the fluid be fairly incompressible and transmit pressure in all directions, a variety of different fluids including water, blood, mesoglea, or coelomic fluid, might serve this function. In most of the models of gastropod locomotion, the blood serves as the antagonist to muscular contraction. The blood has been proposed as a fluid skeleton in *Lymnaea stagnalis* (BEKIUS, 1972), *Haliotis* spp. (CROFTS, 1929), *Helix pomatia* (DALE, 1973), *Agriolimax reticulatus* (=*Deroceras reticulatum*) (JONES, 1973), and *Patella vulgata* (JONES & TRUEMAN, 1970), although, in the last example, what were originally identified as hemocoelic vesicles have been demonstrated to be mucous glands (GRENON & WALKER, 1978, 1982). The principle upon which these models are based was introduced by PARKER (1911) in a review of JORDAN (1901) and BIEDERMANN (1905): "The musculature of the snail's foot works against the elastic-walled, fluid-filled cavities of the animal's interior."

VOLTZOW (1985), however, demonstrated that the "open" circulatory system of the foot of the marine prosobranch *Busycon contrarium* (Conrad, 1840) consists of discrete arteries and veins that anastomose throughout the foot in a pattern resembling the "closed" circulatory system of annelids and vertebrates. A network of small spaces delimited by the surrounding muscle and connective-tissue matrix links the arteries and veins. Similar pedal circulatory systems have been observed in a diversity of other marine gastropods (Voltzow, personal observation). Thus, while probably important for expanding the sole region and for maintaining turgor once the foot has expanded, the circulatory system is not isolated from the pedal musculature. It is therefore unlikely that the blood functions as the mechanical antagonist to the muscular contractions of locomotion except in those species such as *Bullia digitalis* that have an exceptionally large fluid-filled cavity in the foot (TRUEMAN & BROWN, 1976, 1987).

As an alternative to these theories, other authors have suggested that one set of muscle fibers within the foot might directly antagonize another without any dependence upon a fluid skeleton. TRAPPMANN (1916), for example, suggested that there might be a direct antagonism between the transverse and longitudinal muscles of the foot of *Helix pomatia*. In response to the active extension mechanism proposed by SIMROTH (1878, 1879), CARLSON (1905) suggested that during the normal locomotion of *Helix dupetithouarsi* Deshayes, the contraction of the transverse and oblique muscles of the dorsal and lateral sides of the body could antagonize and extend the longitudinal muscles.

More recently, BROWN & TRUEMAN (1982) and TRUEMAN & BROWN (1985) have shown that the columellar muscle of a variety of gastropod species contains sets of

transverse and radial muscles that antagonize the longitudinal muscles directly. These three-dimensional muscular antagonism systems have been called muscular-hydrostats by KIER (1982, 1988) and KIER & SMITH (1985), who have identified them in a diverse array of molluscan and vertebrate fleshy organs.

The present study investigates the nature of the gastropod pedal antagonistic system by evaluating the roles of the major structural elements—the muscle, connective tissue, and circulatory system—in two species of prosobranch gastropods, *Busycon contrarium* and *Haliotis kamtschatkana* Jonas, 1845.

MATERIALS AND METHODS
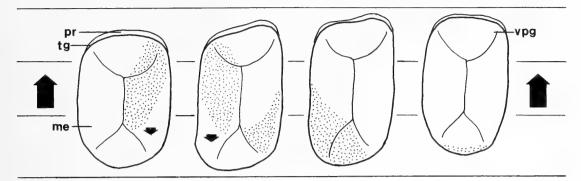
Specimens of the lightning whelk, *Busycon contrarium* (Conrad, 1840), ranging in shell length from 67 to 235 mm were collected at Beaufort, North Carolina, and Alligator Harbor, Florida, USA. Specimens of the pinto abalone, *Haliotis kamtschatkana* Jonas, 1845, were collected from San Juan Island, Washington, USA. Abalone ranged in length from 48 to 130 mm. Individuals of both sexes from both species were used. This study incorporates information gained from observations of over 50 *Busycon* and 15 *Haliotis,* as well as observations of over 20 additional species of gastropods and chitons.

Because *Busycon* is slow to emerge from its shell when disturbed, and because it retracts at any slight disturbance, I experimented with a variety of narcotization techniques. Alcohol, succinyl choline chloride, MS 222, Nembutal, propylene phenoxetol, and asphyxiation either caused snails to retract immediately into their shells or were too weak to have any effect at all. Therefore, to compare the arrangement of the musculature of expanded, crawling snails with retracted ones, some animals were frozen with liquid nitrogen as they crawled, others were narcotized most successfully with a 7.5% magnesium chloride solution, and others were fixed fresh in the retracted position.

To study the gross organization of the muscle fibers, sections several millimeters thick from fresh and fixed specimens were cut with a razor blade and traced with a camera lucida on a Wild M5 stereomicroscope. Specimens were sectioned in the sagittal, transverse, and frontal planes.

To mark the pedal circulatory system, a mixture of India ink in gelatin and water was injected into the pedal artery of smaller specimens and slices of feet. These pieces were fixed in a solution of 2.5% glutaraldehyde and 4.0% formalin in a 0.1 M phosphate buffer at pH 7.2. Experiments with fixatives of a range of osmotic concentrations indicated that this combination minimized shrinking or swelling of the tissue. The fixative's osmotic concentration was measured with a Wescor Inc. 5100C vapor pressure osmometer and adjusted to 735 mOs by adding saturated sucrose solution or distilled water. After dehydration in an alcohol series, the samples were embedded in JB-4 plastic embedding medium (Polysciences, Inc.). Sections 1–7 μm thick were cut with a Sorvall JB-4 microtome using a glass

anterior

posterior

Figure 1

Diagram of the ditaxic retrograde locomotor wave pattern on the sole of *Busycon contrarium*. Large arrows indicate the direction in which the animal is moving, small arrows the direction of movement of waves. Stippled areas are those undergoing movement in each step of the passage of a wave. Pedal length varies in this species from a few millimeters to over 170 mm. me = mesopodium; pr = propodium; tg = transverse groove; vpg = ventral pedal gland.

knife. These sections were stained with toluidine blue and photographed with a Leitz Orthoplan-Pol/Orthomat polarizing photomicroscope.

Serial sections were prepared from specimens that had either been relaxed with magnesium chloride or frozen with liquid nitrogen while crawling. These were fixed in either Bouin's, Zenker's (HUMASON, 1979), or the glutaraldehyde-formalin fixative described above. After being dehydrated in alcohol and cleared in xylene or toluene, samples were embedded in Paraplast (m.p. 56-57°C), a compound of paraffin and plastic polymer, and sectioned at thicknesses varying from 5 to 10 μm. One large, whole specimen of *Busycon contrarium* was sectioned on a sliding microtome; section thicknesses ranged from 10 to 30 μm. Paraplast sections were stained with a Mallory or Milligan trichrome stain (HUMASON, 1979).

To study the detail of the entire muscular system, one specimen of *Busycon* was reconstructed photographically. The expanded foot was cut into 36 cubes, and alternate cubes were sectioned and stained. One representative section from each of 15 cubes was photographed with a compound microscope and reconstructed photographically to a final magnification of 160×. The resulting 0.5-m² photographic montages were suspended in a staggered array that approximated their relative positions in the foot. The entire reconstruction required over 150 pieces of 8 × 10-inch photographic paper and fills a small room.
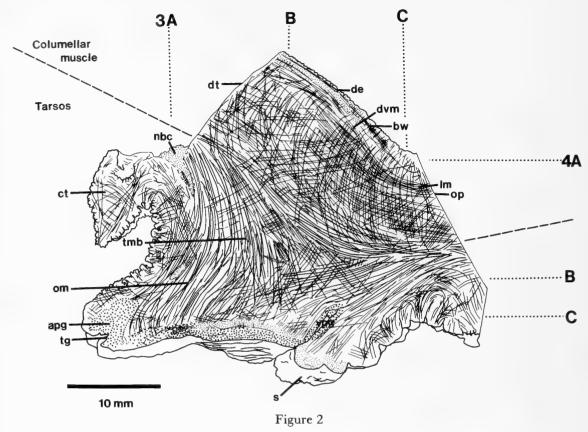
RESULTS

Natural History Observations

Busycon contrarium lives in the intertidal and subtidal zones along the Atlantic coast from New Jersey to Florida and the Gulf of Mexico (ABBOTT, 1974). It uses an in-

distinct retrograde ditaxic locomotor wave to crawl on and burrow into soft substrates (Figure 1). Crawling speeds range from about 0.05 to 0.15 m/min (VOLTZOW, 1986). At the anterior end of the foot, a transverse, ciliated groove separates the propodium from the mesopodium, which is divided into anterior, left, right, and posterior fourths. During crawling, and also during periods of rest between crawling phases, the propodium undulates and probes the substrate in front of it. After a probing phase, the left and right portions of the mesopodium advance alternately by means of a faint retrograde wave of localized contraction along each side, moving the anterior portion with them. The posterior fourth of the foot then advances as if it were simply dragged along, and the cycle begins again. When burrowing, *Busycon* moves its foot ahead into the sand, then brings its shell forward over the already advanced foot. *Busycon* uses its foot to overcome, grasp, and manipulate its prey, which include slow-moving or stationary bivalves such as *Mercenaria mercenaria* (Linné, 1758) and *Crassostrea virginica* (Gmelin, 1791). It forcefully contracts its foot to chip the shell of its prey with the edge of its own shell (CARRIKER, 1951, and personal observation). Females have a ventral pedal gland that they use to give their egg capsules their final species-specific shape and to anchor them to the sand in long strings.

Haliotis kamtschatkana uses direct ditaxic waves (described by LISSMANN [1945] for *H. tuberculata* Linné) to crawl on hard substrates at speeds of over 0.2 m/min. It lives in the intertidal and subtidal zones from Japan and southern Alaska to Point Conception, California (ABBOTT, 1974) and feeds on brown macroalgae such as *Nereocystis luetkeana*. If its cephalic tentacles contact overlying pieces of algae, an abalone can rear up on the posterior portion of its foot and fold the sides of the anterior region together

Figure 2

Camera lucida drawing of the musculature in a mid-sagittal section of a female *Busycon contrarium* head-foot. (Unless otherwise indicated, all figures are oriented so that anterior is left and dorsal is top.) Large stipple = glandular tissue; medium stipple = areas of connective tissue in which muscle fibers were too small to discern; small stipple = blood vessels; dashed lines = division between the columellar muscle region and tarsos; dotted lines = approximate positions of transverse and frontal sections of Figures 3 and 4. apg = anterior pedal gland; bw = body wall musculature; ct = cephalic tentacle; de = pedal dorsal epithelium; dt = cut margin at dorsal trunk of foot; dvm = dorsoventral muscle; lm = longitudinal muscle; nbc = nerve and blood vessel channel; om = oblique muscle; op = cut surface of operculum site; s = sole; tg = transverse groove; tmb = tarsic muscle bundles; vpg = ventral pedal gland.
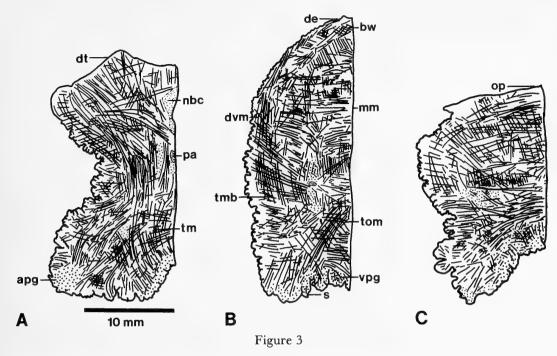
like two hands to grasp the alga in a deep groove aimed at its mouth. When touched by a potential predator, such as the seastar *Pycnopodia helianthoides*, *Haliotis* responds by lifting and twisting its shell from side to side, clamping down on the substrate, or galloping away using locomotor waves of increased amplitude and frequency.

Pedal Musculature of *Busycon contrarium*

Internally, the *Busycon* foot consists of two distinct regions, the dorsal columellar muscle region and the ventral tarsos, which includes the sole (Figure 2). Previous studies of the gastropod foot have identified the columellar muscle but have not used any name for the rest of the foot. I have chosen the word "tarsos," which is a Greek term for the flat of the foot or a flat woven basket, to refer to this structure. In sagittal sections of fresh, protracted specimens, these two regions show distinct differences in color, texture, and shine. When touched, pulled, or chewed (sliced

Busycon is served as "snail salad" in Rhode Island, USA), the columellar muscle is tough and the tarsos is spongy. In transverse section, the border between the columellar muscle and the tarsic region is less distinct (Figure 3). The two regions form one tightly connected entity; one cannot be lifted away from the other, for some of the muscle fibers from the columellar muscle pass into the tarsos.

Frontal sections show that the foot of *Busycon* is a meshwork of transverse, dorsoventral, and oblique muscle fibers (Figure 4). The large number of incomplete muscle fibers in any one figure indicates the extent to which the fibers are oriented obliquely to, rather than parallel to, the anteroposterior and dorsoventral axes of the foot. In section, individual muscle fibers could be called transverse, longitudinal, or dorsoventral, depending upon their orientation in the plane of the particular section. Through its entire length, however, a muscle fiber may in fact be oriented in several different directions, and these directions

Figure 3

Camera lucida drawing of the musculature in transverse sections of a female *Busycon contrarium*. See Figure 2 for section locations in foot and explanation of stippling. apg = anterior pedal gland; bw = body wall musculature; de = pedal dorsal epithelium; dt = cut margin at dorsal trunk of foot; dvm = dorsoventral muscle; mm = cut margin at midline of foot; nbc = nerve and blood vessel channel; op = cut surface of operculum site; pa = pedal artery; s = sole; tm = transverse muscle; tmb = tarsic muscle bundles; tom = transverse oblique muscle; vpg = ventral pedal gland.

are rarely in an absolutely horizontal or vertical plane. The extent to which muscle fibers change directions can be seen by comparing the differences between sections A, B, and C of Figures 3 or 4. Within any one orthogonal section, the majority of muscle fibers are oblique with respect to the plane of section and to the epithelial surface where they insert.
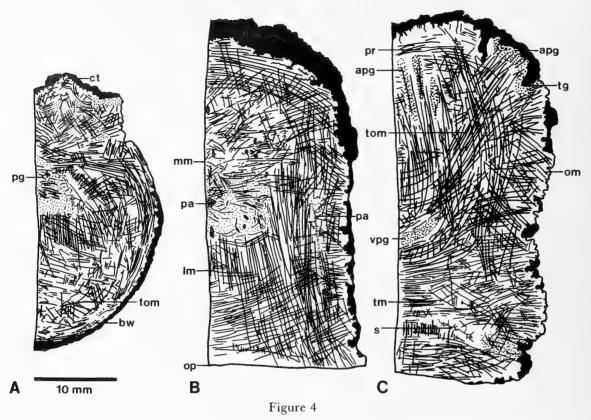
The columellar muscle occupies the dorsal portion of the foot. It appears shiny and white in fresh preparations and contains a lattice of interwoven bundles of muscle fibers (Figures 2, 5). The majority (approximately 70%) of these bundles extend from the muscle's origin on the columella to its insertion on the operculum. In addition to these longitudinal fibers, within the columellar region other bundles of muscle fibers are oriented anterodorsal to posteroventral, posterodorsal to anteroventral, and directly dorsoventral (Figures 2, 5).

The dorsal border of the columellar region includes a layer of connective tissue with several thick, longitudinal muscle fibers and a scattering of thin dorsoventral muscle fibers (Figures 2, 3, 5). Dorsal to this layer, the foot is bounded by the body wall musculature (Figure 5A) and an epithelium. The ventral edge of the columellar region is delineated by a layer of shiny, parallel muscle fibers that extend anteroposteriorly from the columella to the operculum (Figure 2). The longitudinal muscle fibers of this layer are encased in thick connective-tissue sheaths and

are divided into bundles by transverse and oblique muscle bundles.

The tarsos of *Busycon* consists of systems of oblique muscle fibers that interweave to form a complex three-dimensional network (Figure 6). From the surface of the anterior ventral edge of the columellar region, bundles of muscle fibers extend ventrally, branching into finer and finer units that radiate anteriorly, laterally, and posteriorly throughout the anterior two-thirds of the foot (Figure 2). These bundles eventually penetrate the sides and sole of the foot as individual muscle fibers (Figure 6E). From the surface of the posterior ventral side of the columellar muscle, similar bundles of muscle fibers divide into branches that spread anteriorly and ventrally until they, too, penetrate the sole as individual muscle fibers. In the central third of the foot, these two systems interweave.

Although not directly comparable between one animal and another (large animals tend to have relatively more thick muscle fibers, small animals tend to have relatively more thin ones), within the same animal the individual muscle fibers of the columellar region tend to have a larger diameter than those of the tarsos. Within one specimen of *Busycon contrarium* whose shell length was 95 mm, the columellar muscle fibers ranged in diameter from 3.1 to 4.4 μm. Those in the tarsos were about 1.7 to 3.4 μm. In another specimen whose shell length was approximately 150 mm, muscle fibers measured 7.4 to 11.1 μm in diameter

Figure 4

Camera lucida drawing of the musculature in frontal sections of a female *Busycon contrarium*. See Figure 2 for section locations in foot and stippling explanation. Anterior is at top of figure. A is more dorsal, C more ventral. Solid shading = epithelium on outer surface; apg = anterior pedal gland; bw = body wall musculature; ct = cephalic tentacle; lm = longitudinal muscle; mm = cut margin at midline of foot; om = oblique muscle; op = cut surface of operculum site; pa = pedal artery; pg = pedal ganglion; pr = propodium; s = sole; tg = transverse groove; tm = transverse muscle; tom = transverse oblique muscle; vpg = ventral pedal gland.
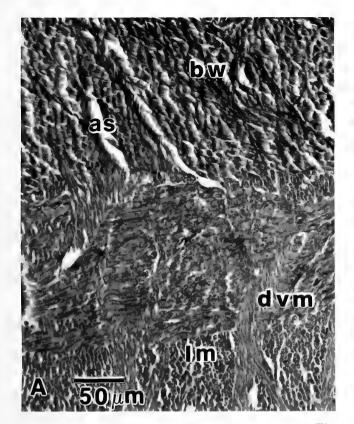
in the columellar muscle and 2.6 to 4.4 μm near the pedal epithelium.

Pedal Musculature of *Haliotis kamtschatkana*

Like the foot of *Busycon contrarium,* the foot of *Haliotis kamtschatkana* is composed of two distinct portions, the columellar region and the tarsos (Figures 7, 8). Unlike the situation in *Busycon,* however, the tarsic region in *Haliotis* surrounds the columellar region anteriorly, posteriorly, and laterally. The central core of the foot is composed of the hypertrophied right columellar muscle, which has its origin on the broad ventral surface of the shell and inserts on the sole epithelium. Thus, the long axis of the muscle is oriented perpendicular to the animal's anteroposterior axis. The majority of the muscle fibers in the columellar region lie in dorsoventral bundles. Dispersed among these are bundles of radial muscle fibers, and distributed through and around these two systems is a third system of concentric circular muscle fibers (Figures 7–9). The circular muscles are distributed around the periphery of the columellar region, while the radial muscles are more concentrated

near its center. Some of the circular muscles may be helically oriented, wrapping the columellar muscle region in a discontinuous sheath of helically oriented muscle bundles. At least some of the radial muscle fibers are oriented in a direction oblique to, rather than strictly perpendicular to, the long axis of the columellar muscle.

Sagittal and transverse sections through a *Haliotis* foot show that the columellar region is bordered by the thick muscle bundles of the tarsos (Figure 10A), which radiate from their origin on the shell and divide into smaller and smaller branches that eventually penetrate the pedal epithelium at the sides and sole (Figures 7, 8, 11, 12). At the outer edge of the columellar muscle, these bundles branch into smaller bundles whose muscle fibers pass directly dorsoventrally through the foot and insert at the sole epithelium. Distal to these bundles, smaller branches spread slightly more laterally and become interspersed with the branches of neighboring bundles (Figure 11). At the sides of the foot, these finer branches spread laterally and ventrally, and penetrate the epithelium at oblique angles (Figure 12). Posteriorly, some of the smaller branches extend
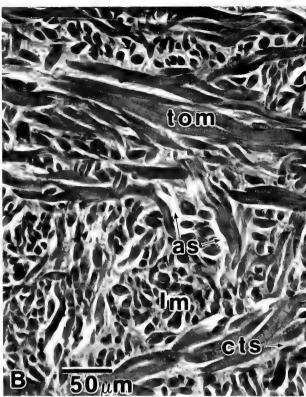
Figure 5

Photomicrographs of details from a section of the columellar muscle region of *Busycon contrarium*. Specimen was frozen in liquid nitrogen while crawling, fixed in glutaraldehyde-formalin, and stained with Milligan trichrome stain. A. Dorsal body wall. B. Thick muscle fibers of the interior of the muscle. Note than A and B have the same scale and show artificial spaces caused by paraffin embedding. as = artificial space; bw = body wall musculature; cts = connective-tissue sheath; dvm = dorsoventral muscle; lm = longitudinal muscle; tom = transverse oblique muscle.

almost horizontally, so that they fill the posterior portion of the foot with oblique, dorsoventral, and anteroposterior muscle fibers. In addition to these muscle fibers, the ventral portion of the sole contains some isolated transverse or obliquely transverse muscle fibers that appear not to be a part of the branching systems.

Pedal Connective Tissue

All of the muscle fibers of *Busycon* and *Haliotis* are wrapped in connective-tissue sheaths. These sheaths are quite distinct in sections stained with Mallory or Milligan trichrome, in which muscle is red and connective tissue is blue or blue-green (Figure 10). In fact, the foot is virtually solid muscle wrapped in connective-tissue sheaths (Figures 5, 6, 10–13). When viewed with polarized light microscopy, these sheaths are birefringent, indicating that they are anisotropic (Figure 13), and that the preferred orientation of the molecules composing the sheaths is parallel to the long axis of the muscle fibers. Preliminary information from amino acid analysis (performed on samples

of *Busycon* and *Haliotis* pedal tissue by Dr. John Abernathy of the Duke University Department of Pathology) indicates by its imino acid content that the sheaths have a collagen component. Scanning electron microscopy (SEM) of muscle from *Haliotis* indicates that the sheaths are composed of parallel arrays of collagen fibers that are oriented parallel to the long axis of the muscle fibers they surround (Figure 14).

Within the columellar region of both species, the bundles of muscle fibers are wrapped in thin connective-tissue sheaths (Figures 5, 10). Virtually no other extracellular connective tissue is present. In the tarsic region, on the other hand, as the individual fibers within the bundles become smaller, the connective-tissue sheaths become thicker (Figure 10B, C), and the amount of extracellular connective tissue, both sheaths and seemingly unorganized matrix, increases towards the periphery of the foot (compare, for example, Figure 10 with Figure 12). The fine ramifications that insert at the sole are probably individual muscle fibers and are embedded in a dense connective-tissue matrix.
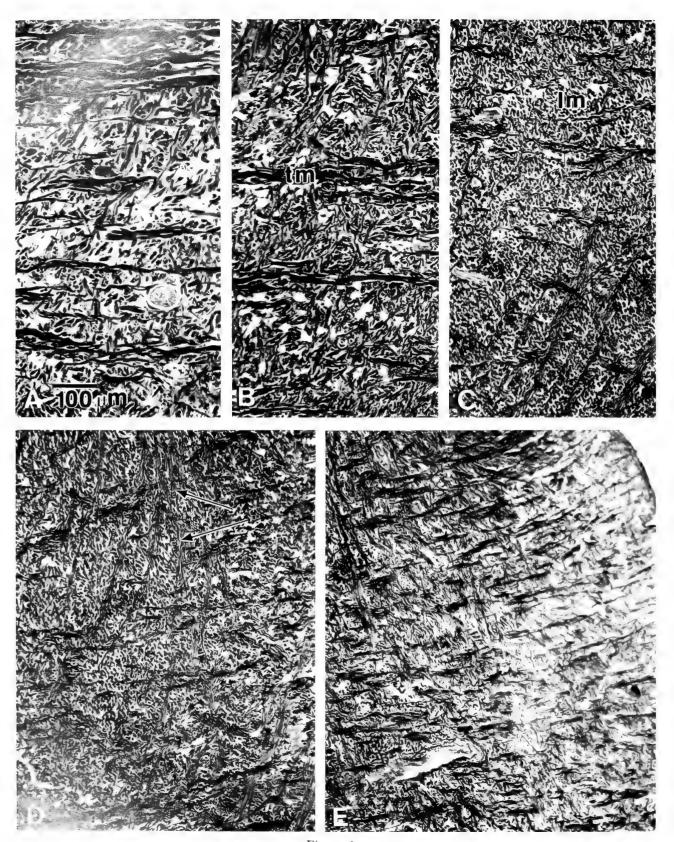
Figure 6

Photomicrographs from different areas of a 5-µm-thick transverse section through the tarsos of *Busycon contrarium* illustrating the decrease in muscle bundle size as the bundles spread from the interior (A) to the lateral epithelium (E) of the foot. Specimen prepared as in Figure 5. Note the branching of the dorsoventral (D, arrows) and transverse (E) muscle bundles. lm = longitudinal muscles; tm = transverse muscles.
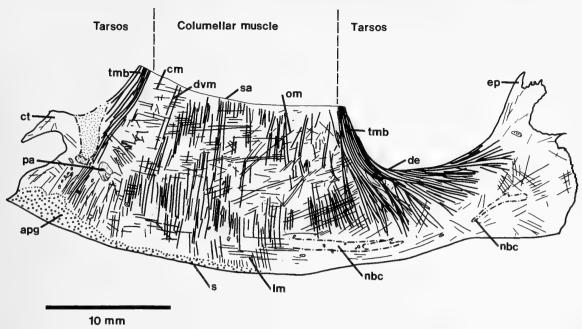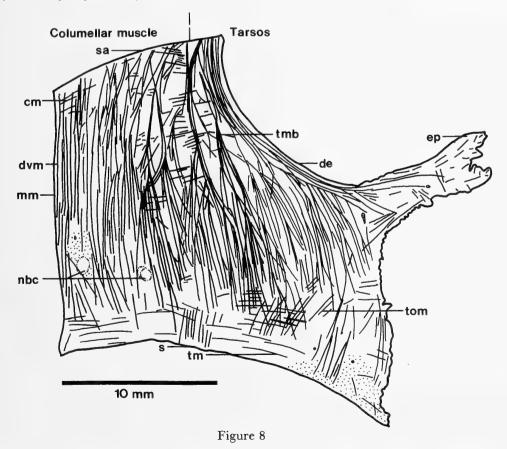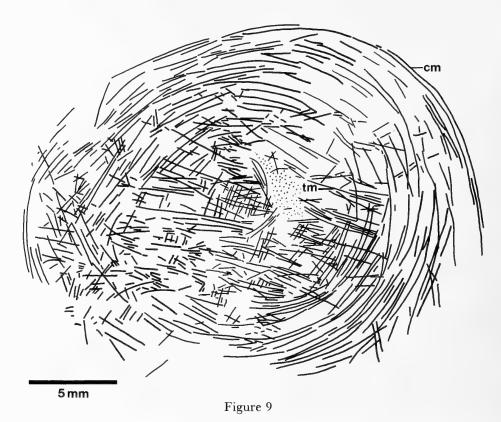
Figure 7

Camera lucida drawing of the musculature in a mid-sagittal section of a *Haliotis kamtschatkana* head-foot. Stippling as in Figure 2. apg = anterior pedal gland; cm = circular muscle; ct = cephalic tentacle; de = pedal dorsal epithelium; dvm = dorsoventral muscle; ep = epipodium; lm = longitudinal muscle; nbc = nerve and blood vessel channel; om = oblique muscle; pa = pedal artery; s = sole; sa = cut surface of shell attachment site; tmb = tarsic muscle bundles.

Figure 8

Camera lucida drawing of the musculature in a mid-transverse section of *Haliotis kamtschatkana*. Stippling as in Figure 2. cm = circular muscle; de = pedal dorsal epithelium; dvm = dorsoventral muscle; ep = epipodium; mm = cut margin at midline of foot; nbc = nerve and blood vessel channel; s = sole; sa = cut surface of shell attachment site; tm = transverse muscle; tmb = tarsic muscle bundles; tom = transverse oblique muscle.

5 mm

Figure 9

Camera lucida drawing of the musculature in a frontal section of the columellar muscle region of *Haliotis kamtschatkana*. The left side of the section is anterior and slightly more dorsal than the right. cm = circular muscle; tm = transverse muscle.

DISCUSSION

General Pattern of Pedal Muscular Organization

In both *Busycon contrarium* and *Haliotis kamtschatkana,* the foot consists of two distinct regions, the columellar muscle region and the tarsos. The columellar region consists primarily of muscle fiber bundles that are oriented parallel to the long axis of the muscle. In *Busycon,* this is a longitudinal direction in the expanded foot, in which the columellar muscle connects the columella with the operculum. In *Haliotis,* the major axis of the columellar region is dorsoventral, as is the majority of the muscle fibers comprising it. In addition, the columellar region of both species contains muscle bundles that are oriented perpendicular to the long axis of the muscle in at least two directions. In *Busycon,* these muscles are oriented in the oblique diagonal and radial directions; in *Haliotis* they are arranged in circles around the columellar muscle and in the radial directions as well.

In contrast to the columellar region, the tarsic region consists of bundles of muscle fibers that branch and change direction as they extend from their origins to their insertions. They form a complex three-dimensional network of interconnecting contractile fibers. The bundles become finer and finer as they approach the periphery of the foot and become more and more deeply embedded in the connective

tissue of the ventral and lateral extremities. It is not clear at the light microscope level whether the decrease in bundle size is due to a decrease in cell diameter, a decrease in the number of cells per bundle, or both.

The Relationship Between Structure and Function

The structural differences between the two regions of the foot are reflected in their functions. The columellar muscle is primarily involved in producing major body movements and changes in shape and posture: protraction, retraction, twisting, elevating and lowering the shell, and clamping onto the substrate. Pressures generated by the forceful contraction of the columellar muscle in *Busycon* and *Haliotis* are quite large (over 3 kPa) and rapid (VOLTZOW, 1986). The functional system of a columellar muscle containing fibers that are arranged in a three-dimensional antagonistic network appears to be a fundamental one for prosobranch gastropods (BROWN & TRUEMAN, 1982; TRUEMAN & BROWN, 1985; VOLTZOW, 1986; KIER, 1988). Contraction of the bundles whose long axes are parallel to the long axis of the muscle results in retraction of the snail into its shell, as in *Busycon,* or in a reduction of the distance between the body and the substrate, as in *Haliotis.* More muscle fibers have this orientation than any other in the foot; their contraction appears
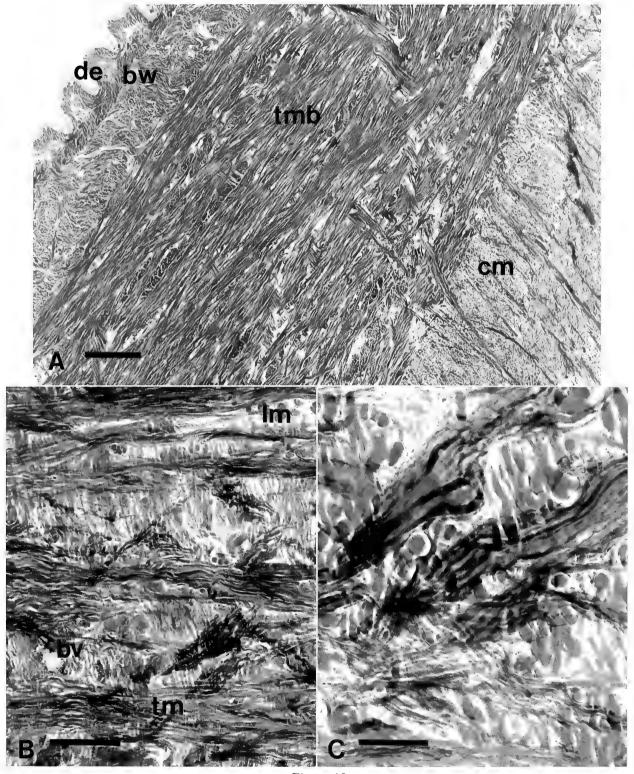
Figure 10

A. Photomicrograph of a 7-μm-thick sagittal section through the edge of the foot of *Haliotis kamtschatkana* showing the pedal epithelium and body wall musculature (upper left), the tarsos (center), and the columellar muscle region (lower right). Specimen was fixed in glutaraldehyde-formalin, embedded in Paraplast, and stained with Milligan trichrome stain. Muscle is red; connective tissue is blue. Scale bar = 200 μm. B. Photomicrograph of a 10-μm-thick transverse section through the transition between the columellar muscle region and the tarsos of *Busycon contrarium*. Transverse muscles at the top of the figure lie at the ventral edge of the columellar region. Specimen prepared as in Figure 5. Scale bar = 100 μm. C. Detail from section shown in B. Scale bar = 50 μm. bv = blood vessel; bw = body wall musculature; cm = circular muscle of the columellar region; de = dorsal pedal epithelium; lm = longitudinal muscle; om = oblique muscle; tm = transverse muscle; tmb = tarsic muscle bundles.

Figure 11

Photomicrograph of branching muscle bundles from a 5-μm-thick sagittal section of the tarsic region of *Haliotis kamtschatkana*. Specimen was narcotized with magnesium chloride, fixed with glutaraldehyde-formalin, embedded in JB-4, and stained with toluidine blue. Note the absence of artificial spaces.

to be the most forceful action the foot undergoes. Assuming that the columellar muscle has a constant volume, then if the major retractor muscles relax, contraction of the transverse, radial, or circular bundles will result in protraction or an increase in the distance between the shell and the substrate. The circular muscle of *Haliotis* would be particularly effective in lifting the shell above the substrate.

In addition, at least some of the circular and transverse fibers appear to be helical. If they are arranged in left- and right-hand helices, then these muscles could also bring about the twisting action described in *Haliotis* and a similar twisting movement I observed in *Busycon*. The muscle fibers of the columellar region appear to play little or no part in the fine motor function of the rest of the foot. The

Figure 12

Photomicrograph of muscle fibers inserting at the sole epithelium from a 5-µm-thick sagittal section of the tarsos of *Haliotis kamtschatkana*. Specimen prepared as in Figure 11. Note that the lighter areas within the section are filled with connective tissue and are not artificial spaces. bw = body wall musculature; cts = connective-tissue sheath; lm = longitudinal muscle; om = oblique muscle; s = sole.

locomotor waves of *Haliotis,* for example, are restricted to the outer edges of the foot and do not pass through the portion of the sole where the columellar muscle inserts.

The tarsic musculature is involved in the fine movements of locomotion and food manipulation. Local contractions of the tips of several bundles probably produce the locomotor waves, which are accompanied by local fluctuations in pressure (VOLTZOW, 1986). By controlling the number

of branches within a bundle and the number of bundles recruited, a gastropod should have a great deal of control over its fine motor functions. Over its entire course, a bundle may change directions, starting out with a dorso-ventral orientation and eventually having an oblique or transverse orientation. The splitting of the bundles probably permits greater flexibility and variability in the movement of the foot. A large movement may be effected by
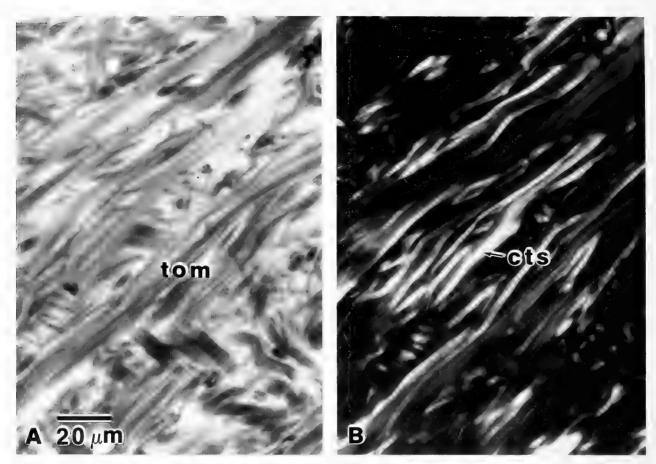
Figure 13

Photomicrographs taken with non-polarized (A) and polarized (B) light of muscle fibers and their connective-tissue sheaths from a 5-μm-thick sagittal section through the tarsic region of *Haliotis kamtschatkana*. Specimen prepared as in Figure 11. JB-4 is not birefringent, and the stain in the muscle fibers interferes with the birefringence, so that only the connective-tissue sheaths are visible with polarized light microscopy. cts = connective-tissue sheath; tom = transverse oblique muscle.

simultaneous contraction of all of the muscle fibers of several bundles. Finer movements should require only a few of the finest branches to be recruited.

Similar networks of branching bundles of muscle fibers have been noticed in the feet of several species of gastropods. WEBER (1926), for example, observed that in *Nassarius mutabilis* (=*Nassa mutabilis*) the muscle bundles divide into finer and finer units so that when they reach the connective tissue of the sole, they are broken up into individual fibers. ROGERS (1969) described the foot muscle of *Helix aspersa* Müller as arranged in bundles that "interweave to form a complex mesh." SCHMIDT (1965) noted that the functional changes of the form of the foot in *Helix pomatia* depend upon the lattice structure of the musculature. He stressed that the foot be analyzed as a functional system, a muscular antagonism system ("*muskularen Systemantagonisten*"), rather than as a set of isolated muscle fibers.

The Role of the Connective Tissue in Pedal Function

Essential to the meshworks of both the columellar muscle region and tarsos are the connective-tissue sheaths surrounding the muscle fibers. In the columellar region, the sheaths are relatively thin; in the tarsos, the sheaths increase in thickness as the bundle diameters decrease until individual muscle fibers are embedded in a dense matrix of connective tissue.

The connective tissue system has, until now, been omitted from studies of pedal functional morphology. While the details of its attachments to the muscle fibers and its ultrastructure are still unclear, the connective tissue system undoubtedly plays an important role in pedal function. At the gross level, the connective tissue contributes to the tough but flexible form of the foot and gives the foot its stretchy, elastic properties. As sheaths of oriented fibers around the muscle, the collagen provides each muscle with its own

tendon, and probably helps transmit forces from one portion of a bundle to another. Antagonism between opposing bundles could be aided by the anastomosis of the collagen fibrils between the sheaths of neighboring muscle cells. The mechanism for this rests, in part at least, with the connective tissue connection between the muscle fibers and their sheaths, and between the antagonizing muscle bundles and their attachments. The increase in volume fraction of connective tissue at the periphery of the foot probably provides the increased flexibility and deformability of this region, because the action of each muscle fiber can be amplified by the passive action of the connective tissue around it.

Bundles of muscle fibers bound together by connective tissue similar to those described here for *Busycon* and *Haliotis* were observed in the foot of *Patella* by Davis & Fleure (1903). Schmidt (1965) observed that the muscle fibers of *Helix pomatia* were surrounded by fibers that were collagenous or that greatly resembled collagenous fibers: single fibrils had crossbands at regularly discernible distances of about 63 nm (collagen has a characteristic periodicity of approximately 67 nm [Woodhead-Galloway, 1980]). Unfortunately, he did not discuss the collagen orientation with respect to the muscle fiber. Each muscle fiber in the feet of *Neritina reclivata* and *Thais rustica* has a connective-tissue sheath (Gainey, 1976). In the foot of *Polinices lewisi* (Gould), Bernard (1968) saw that all the muscles were ensheathed with collagen-reaction type connective tissue. Sminia (1972) saw a network of connective-tissue fibers around the muscle fibers of *Lymnaea stagnalis*. These fibers stained with aniline blue and by silver impregnation, so they are probably collagen and/or reticulin (procollagen) fibrils. Silver impregnation staining of *Lymnaea* sections also indicated to Plesch et al. (1975) that each muscle cell was surrounded by a fine network of reticulin fibers. Plesch (1977) found that the muscle cells of *L. stagnalis* are organized in a meshwork and are anchored to the connective tissue surrounding them by hemidesmosome-like structures. She made no mention of fiber angles, either between collagen fibers or between collagen and muscle fibers. Her study is the only ultrastructural information available on the connections between gastropod pedal muscle fibers or between the fibers and their connective-tissue sheaths. Although all of these authors observed the connective-tissue sheaths, none made any attempt to understand their function. In addition, none of the models of gastropod locomotion discussed in the introduction make any mention of connective tissue. More information about the fine structure and precise orientation of the collagen sheaths and their connections is necessary to understand how the connective tissue transmits the forces of contraction in the foot.

Scanning electron microscopy of muscle from the foot of *Haliotis kamtschatkana* and amino acid analysis of both gastropod species indicate that the sheaths around the muscle cells are composed of parallel arrays of collagen very similar to those illustrated in vertebrate tissue by Nagel
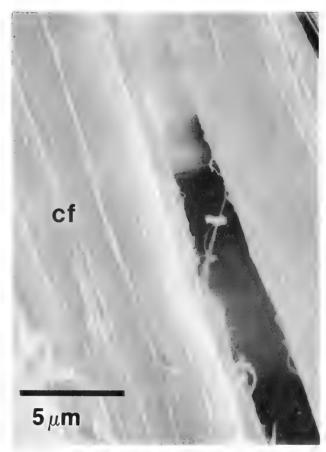
Figure 14

Scanning electron micrograph of the columellar muscle of *Haliotis kamtschatkana* showing collagen fibers forming a sheath around the muscle fibers. cf = collagen fiber.

(1934, 1935), Borg & Caulfield (1980), and Winegrad & Robinson (1978). If the sheaths described for *Busycon* and *Haliotis* are composed of parallel arrays of collagen fibers oriented strictly parallel to the long axis of the muscle fibers they surround, they may be acting as a tendon around the muscle fiber to prevent its over extension. The sheaths may also serve to link one set of muscle fibers with another, distributing the force of contraction or extension, as has been proposed for similar vertebrate systems by Nagel (1934, 1935), and Winegrad & Robinson (1978). In addition, I propose that these connective-tissue sheaths provide the mechanism by which one set of muscle fibers can directly antagonize another by transmitting compressive and tensile forces.

The Prosobranch Foot as a Hydrostatic Skeleton

The gastropod foot has traditionally been viewed as a hydrostatic organ. A hydrostatic skeleton is one in which

body fluid provides the means by which the contractile elements are antagonized (CHAPMAN, 1958). Although, as Chapman has pointed out, any incompressible fluid that transmits pressure in all directions can function as a hydrostat, the usual candidate is a large, fluid-filled space, such as the coelom of annelids or the coelenteron of cnidarians. In models of gastropod locomotion, the circulatory system, or hemocoel, is usually considered the hydrostat. Thus, the transmission of pressure via the hemocoel and its role in muscular antagonism have become a central tenet in accounts of locomotor wave propagation and burrowing (TRUEMAN, 1983).

The pedal circulatory systems of *Busycon* (VOLTZOW, 1985) and *Haliotis* (CROFTS, 1929; BOURNE & REDMOND, 1977) consist of distinct arteries and veins. Only at their finest ramifications do the vessels appear to lack any walls of their own; here they are delimited by the muscle and connective tissue surrounding them. In both species, the columellar muscle region and tarsos receive blood from separate branches of the anterior aorta. There appears to be no mixing of blood between the two portions of the foot. The most extensively vascularized area is the region just dorsal to the sole, where an elaborate system of small, branching vessels penetrates the channels between the muscles and connective tissue. Even in this region, however, the blood occupies only approximately 7% of the total volume of the expanded foot (VOLTZOW, 1985).

Most histological techniques cause shrinkage and distortion that tend to occlude cavities or to create artificial ones. In sections in which the tissue was fixed in Bouin or Zenker and embedded in paraffin, small spaces appeared between the muscle fibers. These spaces resembled those that previous authors have labeled hemocoel in similarly prepared sections of the gastropod foot. In sections fixed in the osmotically controlled glutaradehyde-formalin fixative and embedded in paraffin, the spaces were somewhat reduced (*e.g.,* Figure 5). Those embedded in JB-4 essentially lacked these spaces (*e.g.,* Figure 11). From these sections it is clear that the foot is predominantly solid muscle wrapped in connective-tissue sheaths. Although I have not studied the species described by others, I have examined the feet of at least 20 species of chitons and gastropods using vascular injections and dissections (VOLTZOW, 1985, and personal observation). Although TRUEMAN & BROWN (1976) have demonstrated that an extensive pedal hemocoel does exist in *Bullia,* I believe that much of what has been identified as hemocoelic space in the feet of other marine prosobranchs is actually artifact due to the shrinkage associated with fixation and paraffin embedding.

The arrangement of the muscles in the columellar muscle makes it possible for them to antagonize each other. Thus, the columellar muscle is a muscular–hydrostat (*sensu* KIER & SMITH, 1985). Although the blood in the tarsos does not usually occupy a large central cavity, it does probably contribute to the overall turgor of the foot by filling the many fine vascular channels. The tarsos is not

as solid a muscular organ as is the columellar muscle. Instead, the tarsic regions of *Busycon* and *Haliotis* are hydrostatic systems in which the role of the body fluid is intermediate between that of a classic hydrostatic cavity and muscular–hydrostat.

Throughout the diversity of species of prosobranchs, the extent of vascularization of the tarsic region appears to be quite variable. Limpets such as *Patella vulgata* and *Tectura scutum* (Rathke, 1833) (=*Notoacmaea scutum*), for example, have a very reduced pedal circulatory system; the entire foot is essentially solid muscle (JONES & TRUEMAN, 1970; VOLTZOW, 1988). TRUEMAN & BROWN (1976), on the other hand, have identified a large blood-filled space in the foot of *Bullia digitalis.* In addition, water-filled, or aquiferous, systems have been described for several species of naticids (BERNARD, 1968; RUSSELL-HUNTER & RUSSELL-HUNTER, 1968; RUSSELL-HUNTER & APLEY, 1968). The tarsos, therefore, probably spans the entire range of possible hydrostatic systems, from the solid muscles of limpets to more fluid-dependent systems such as the highly inflated foot of *Bullia.*

Evolutionary Trends in the Functional Morphology of the Prosobranch Foot

There have been at least two major trends in the evolution of the prosobranch foot. First, there has been a repeated convergence upon the limpet shape. In each case, it appears that the muscle system is organized into a series of paired muscle bundles that extend dorsoventrally and spread diagonally as they approach the sole, so that a transverse section of a limpet foot closely resembles that of a monoplacophoran or polyplacophoran (VOLTZOW, 1988). This organization most likely increases the ability of the limpet to adhere to hard substrates, which are the characteristic limpet habitats.

The second major trend is less obvious, but I believe that there has been a tendency toward a reduction of the columellar muscle and a corresponding increase of the tarsic system in non-limpet prosobranchs. The prosobranchs are traditionally divided into three subclasses: Archaeogastropoda, Mesogastropoda, and Neogastropoda. This classification roughly corresponds to the sequence in which the members of the subclasses appear in the fossil record. MILLER (1974b) found that archaeogastropods tend to use rhythmic pedal waves only, mesogastropods use all patterns except diagonal ditaxic waves, and the neogastropods use rhythmic, arrhythmic, and ciliary locomotion. Although prosobranch gastropods are an extremely diverse group, in general, archaeogastropods are characterized by a globose, low spired shell, round shell aperture, and a round sole. Neogastropods tend to have a shell with an elongate aperture and have reduced or lost their opercula. Mesogastropods tend to be intermediate (FRETTER & GRAHAM, 1962; MILLER, 1974a, b; McNAIR *et al.,* 1981; GAINEY & STASEK, 1984), although many neogastropods and mesogastropods show convergence in shell form (SIGNOR,

1985). The shift in shell shape and locomotor type from archaeo- to meso- and neogastropods is usually attributed to a habitat expansion from rocky substrates to sand and mud (YONGE & THOMPSON, 1976). Thus, through evolutionary time, a trend appears, from an operculated, round foot that uses distinct, simple muscular waves to a more elongate shell with a narrow aperture and a foot that lacks an operculum and uses more complex, less distinct waves. Of course, as with any generalization of evolutionary trends there are many exceptions, but certainly, the tarsos of *Busycon* is much more complex and performs a greater range of movements than the tarsos of *Haliotis*. In the feet of non-limpet gastropods that lack an operculum, the columellar muscle loses its integrity and divides into bundles that spread to the anterior, posterior, and ventral parts of the foot (BRACE, 1977). Increases in functional plasticity of the neogastropod foot could be accomplished by the integration of these columellar bundles with the already extensive ramifications of the tarsic muscle fiber arrangement. Thus the entire foot would have the flexibility of the tarsos combined with the force of the columellar muscle. It should be possible to examine more feet and follow the changes that the columellar muscle and tarsos have undergone in the various families to see if this trend has in fact occurred.

SUMMARY

(1) Dissections and histological sections show that the feet of *Busycon contrarium* and of *Haliotis kamtschatkana* consist of two distinct regions, the dorsal or central columellar muscle region and the ventral or peripheral tarsos. Both regions are composed of muscle bundles wrapped in connective tissue sheaths.

(2) The columellar region contains bundles of large-diameter (usually greater than 5 μm) muscle fibers wrapped individually in thin connective-tissue sheaths. Most of the bundles are oriented parallel to the long axis of the muscle. Additional bundles cross the region and form a lattice of radial, transverse, and longitudinal muscle fibers.

(3) The tarsos contains bundles of muscle fibers that divide into smaller and smaller branches as they extend from the dorsal to the ventral portions of the region. As the branches become smaller, the thickness of the connective-tissue sheaths surrounding them becomes greater. The muscles of the tarsos comprise a three-dimensional network of interwoven muscle fibers, mostly of small diameter (usually less than 5 μm), that pass through the foot in oblique, transverse, dorsoventral, and anteroposterior directions.

(4) The muscle bundles of the columellar region appear to be responsible for the major movement of the foot into and out of the shell. They also function to twist the shell from side to side and to lift and lower it relative to the substrate.

(5) The branching muscles of the tarsos are responsible for the fine movements of wave propagation, prey manipulation, and egg capsule shaping.

(6) The connective-tissue sheaths probably play an important role in the antagonism of one muscle set by another.

ACKNOWLEDGMENTS

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The Recent Eastern Pacific Species
of the Bivalve Family Thraciidae

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Abstract. Twenty-two Recent species of thraciids are recognized in the area from the Arctic coast of Alaska to their most southerly known occurrence in northern Peru. *Thracia myopsis* (of which *T. beringi* is a synonym) and *T. devexa* remain in *Thracia* s.l.; *T. trapezoides* and *T. challisiana* are assigned to subgenus *Homoeodesma*; *T. septentrionalis* to subgenus *Crassithracia*; *T. condoni,* here reported from the Recent fauna, to subgenus *Cetothrax*; *T. curta* and *T. anconensis* to subgenus *Ixartia*; and *T. squamosa* and *T. **bereniceae,** new species, to subgenus *Odoncineta*.

Asthenothaerus villosior and *A. diegensis* are separable taxa in *Asthenothaerus* s.s. "*Thracia*" *colpoica* is placed in *A.* (**Skoglundia**), new subgenus. The genus *Bushia* s.s., contains *B. panamensis, B. galapagana* (transferred from *Cyathodonta*), and *B. **phillipsi,** new species. *B.* (**Pseudocyathodonta**) **draperi,** new subgenus and species, is proposed. *Lampeia* is accorded full generic status, with *L. adamsi* its only species. The following taxa are recognized in *Cyathodonta: C. undulata, C. dubiosa, C. pedroana,* and *C. tumbeziana*.

A number of new synonymies and six lectotype designations are made. Information is provided about the distributions and habitats of these species and their possible relationships to taxa of other faunas and in the fossil record.

INTRODUCTION

The purpose of this paper is to discuss the genera and species of the bivalve family Thraciidae that occur from the Arctic coast of Alaska to northern Peru, as far south as any members of the family have as yet been collected. In an earlier note (COAN, 1969), I placed Dall's "*Macoma*" *truncaria* into *Thracia* (*Crassithracia*).

KEEN (1969:850–852) reviewed the genera of the Thraciidae and their type species. The present account differs in the ranking of genera and subgenera, as well as in some details about type species and their designations.

RUNNEGAR (1974) reviewed the evolutionary history of the Anomalodesmata based chiefly on detailed analysis of fossil material, indicating that Mesozoic thraciids had nacreous shells, whereas Recent taxa have granular microstructure[1].

SCARLATO & STAROBOGOTOV (1978) erected a superfamily, the Thracioidea, for just the Thraciidae. BOSS (1978)

discussed the classification of several families of the Anomalodesmata, noting that the Thraciidae, Periplomatidae, and Laternulidae have much in common. YONGE & MORTON (1980) outlined the evolutionary history of the Anomalodesmata, with a particular focus on the ligament-lithodesma complex. They recommended that the Thracioidea include the Thraciidae, Periplomatidae, and Laturnulidae, based on a ligament that is chiefly on a pivotal axis, with an anterior lithodesma that ensures valve alignment. This is in contrast to the situation in the Pandoroidea, in which the ligament is more ventrally placed, the lithodesma aiding in opening the valves.

This separation was further discussed by MORTON (1981, 1985), who summarized the available anatomical information about the Thraciidae. A detailed definition of the family compiled from the literature was provided by BOSS (1982:1159).

Previous treatments of the species of the Thraciidae include those of KIENER (1834), COUTHOUY (1839), REEVE (1859), CONRAD (1869), and LAMY (1931). Other significant historic discussions of the family are those of BLAINVILLE (1825–1827), DESHAYES (1830, 1832, 1846, 1850), HANLEY (1843, 1856), RÉCLUZ (1845, 1846, 1853),

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[1] The iridescence visible on the eroded beaks of some species of *Thracia* (*Homoeodesma*) and on the inside of the valves of *T.* (*Odoncineta*) *speciosa* Angas, 1869, merits further investigation.
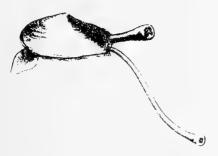
Figure 1

Thracia (Odoncineta) phaseolina (Lamarck). Figure in CosTA (1829: pl. 2, fig. 1) of *Odoncineta papyracea* (Poli).
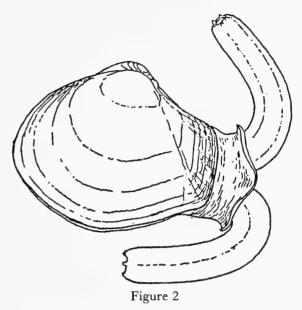
STOLICZKA (1870), FISCHER (1887), DALL (1903, 1915), and LAMY (1925, 1934). KAMADA (1955) reviewed the Tertiary species of Japan.

SooT-RYEN (1941) discussed the northern European species of *Thracia,* differentiating them on the basis of shell shape, resilifer morphology, pallial sinus form, and surface sculpture. ALLEN (1961) discussed the British species, focusing on the hinge-lithodesma complex and on shell shape. (Although most of the British species also occur in the European-Arctic, Allen was evidently unaware of Soot-Ryen's paper.)

COSTA (1829:cxxxi; pl. 2, figs. 1–3) was the first to illustrate a thraciid animal. His figures of what is here called *Thracia (Odoncineta) phaseolina* (Lamarck, 1818) show long, separate siphons and a small, spade-shaped foot (Figure 1). Anatomical illustrations of this species were later published by DESHAYES (1846:pl. 25c). Both authors figured the small lithodesma present under its beaks.

KIENER (1834:pl. 1, figs. a–c) illustrated the anatomy of what appears to be *Thracia (Homoeodesma) convexa* (Wood, 1815), showing long, separate siphons and a small foot. (The evenly oval outline of the shells and Kiener's prominent citation of British localities suggest that the species illustrated was not *T. (H.) corbuloidea* (Blainville, 1827), as he had thought). DESHAYES (1846:pl. 22, figs. 1–3) provided anatomical figures of *T. (H.) corbuloidea* (but under the name *T. convexa,* with which he had mistakenly synonymized it). A description of living specimens of *T. (H.) conradi* Couthouy, 1839, was given by MORSE (1913:75–77; 1919:157–160).

The first observations on living thraciids were those of W. Clark (in FORBES & HANLEY, 1848:222–223; pl. H, fig. 4) and W. CLARK (1855:140), who described the siphons of *Thracia (Odoncineta) phaseolina* as being capable of great inflation. The siphon behavior of this species was later studied by YONGE (1937), who misidentified his material as *T. (T.) pubescens* (Pulteney, 1799). Yonge concluded that the behavior is used for mucus agglutination of sediment particles lining the distal 1 to 2 cm of the tubes, enabling the animal to burrow more deeply and to feed without leaving its siphon tips exposed to predators.

Figure 2

Thracia (Homoeodesma) conradi Couthouy. Figure of MORSE (1913: 76).

This may not explain similar behavior reported in *Thracia (Ixartia) distora* (Montagu, 1803) by W. Clark (in FORBES & HANLEY, 1848:233; pl. H, fig. 5), for this species nestles in rock crevices (FORBES & HANLEY, 1848:234).

On the other hand, this explanation does fit similar behavior reported for *Thracia (Homoeodesma) conradi* by MORSE (1913:75–77; 1919:157–160). Morse also reported an extension of the mantle and periostracum at the posterior end to form a collar around the siphons of this species (Figure 2). Such a structure is not apparent in the above-cited figures of Kiener and Deshayes or in preserved material I have seen of related species.

GUPPY (1875:52) described the siphons of *Cyathodonta rugosa* (Lamarck, 1818) (as "*Thracia dissimilis* Guppy, 1875") as being long, separate, and coarsely fringed. DALL (1886:311) described the body of *Bushia elegans* (Dall). It has short, separate, papillose siphons, a small foot, and a mantle closed ventrally except for the pedal aperture.

MORTON (1985:432–433; fig. 9A) illustrated the position in the substrate of *Trigonothracia jinxingae* Xu, 1980 (pp. 337–339; fig. 1). It is situated posterior end uppermost, the siphons extending to the surface separately.

The natural history of *Thracia (H.) conradi* was investigated by THOMAS (1967), who reported that it lives in muddy sand in 4 m of water, situated 14–26 cm (mean, 17 cm) deep in the sediment, positioned with the more convex, right valve uppermost. The siphons reach the sand surface about 8 cm apart. The ventral, incurrent siphon tends to be surrounded by a mound of sand, whereas the excurrent siphon tends to be in a depression. In the laboratory, the siphons were frequently repositioned, but an animal with a large, inflated shell in proportion to a small foot, stays in place once established.

OCKELMANN (1959) demonstrated that three Arctic species of *Thracia*—*T. devexa, T. myopsis,* and *T. septentrionalis*—are hermaphroditic, with short or absent planktonic stages.

PELSENEER (1911:74–75; pl. 15, fig. 1) discussed and figured the anatomy of a specimen attributed to *Asthenothaerus* ("*Stenothaerus*" on the plate explanation). No shell is figured; no species name is given; and the specimen came from 2798 m, exceptionally deep for a thraciid. Thus, its identity is uncertain.

Thraciid shells are particularly fragile and require special care in curation and study. Many specimens in collections have been broken over the years, in part because many thraciid shells are thin. Even those shells that seem to be sufficiently thick to be sturdy are in fact fragile, probably because all species thus far studied have a two-layered, homogeneous shell structure (TAYLOR *et al.,* 1973: 282–283; table 20; pl. 13, figs. 1–4). In addition, once a specimen is opened for study, care must be exercised to preserve the lithodesma. These have been lost from many museum specimens.

The prominent surface pustules of many thraciids are formed from the outer shell layer (TAYLOR *et al.,* 1973: 283; pl. 13, fig. 4).

GENERAL OBSERVATIONS

A great diversity of hinge morphologies is present in the eastern Pacific bivalves that are placed in the Thraciidae.

The genus *Thracia* includes subgenera in which the internal component of the ligament, and the lithodesma, while visible in juvenile specimens, becomes inconspicuous or undetectable in the adult (*Thracia* s.l., *Homoeodesma, Cetothrax, Crassithracia,* and *Ixartia*). It also includes a subgenus in which the lithodesma is more conspicuous in the adult, *T.* (*Odoncineta*).

In *Asthenothaerus* s.s., and *A.* (*Skoglundia*), there is no external ligament, and the lithodesma is butterfly-shaped. In *Bushia* s.s., *B.* (*Pseodocyathodonta*), and in *Lampeia,* there is a small external ligament and a large lithodesma that fits into a cup under the beaks (lithodesma missing in the only known specimen of *Pseudocyathodonta*). In *Cyathodonta,* there is no internal ligament in the adult, and the external ligament is seated on a thickened, projecting resilifer, a minute lithodesma adhering to its anterior surface.

I hope that the increased information about these eastern Pacific forms, which do not accord well with the current definition of the Thraciidae or of related families, will provide important data for workers concerned about the family and superfamily classifications within the Anomalodesmata.

DISTRIBUTIONS

Among eastern Pacific thraciids, in contrast to many other groups, a high percentage of species seem to have widely disjunct distributions. In part, this may be due to the fact that many species have thin, easily broken shells and live well buried in the sediment, mostly offshore, and are therefore rarely collected. However, this may not provide a complete explanation. Only time and more thorough sampling will show what is the case.

Thracia devexa in British Columbia probably represents a disjunct population from the Arctic Ocean-Bering Sea populations. *Thracia myopsis* is here recorded from a single valve taken off southern California, some 1200 km south of its southern record in British Columbia. *Thracia challisiana* is recorded from stations in southern California and northern Baja California, leaving a gap of about 1100 km from its most southerly occurrence in Puget Sound. *Thracia curta* is known from one pair from Puget Sound and a pair from Vancouver Island, about 830 km north of its otherwise most northerly record at Monterey Bay. *Asthenothaerus digenensis,* which occurs from southern California to Bahía Magdalena, Baja California Sur, has disjunct populations in the central Gulf of California (and there is a pair possibly collected off Oregon).

Bushia galapagana has been obtained only from the Galápagos Islands and Isla del Coco. *Cyathodonta undulata* is known from the Galápagos from a single valve. Otherwise, no other thraciids have been collected from Clipperton, Cocos, or the Galápagos Islands.

FORMAT

In the following treatment, each valid taxon is followed by a synonymy, information on type specimens and type localities, notes on distribution and habitat, and additional discussion.

The synonymies include all major accounts of the species, but not most minor mentions in the literature. The entries are arranged in chronological order under each species name, with changes in generic allocation from the previous entry, if any, and other notes in brackets.

The distributional information is based on specimens I have examined, except as noted. For many species, the available habitat information is unfortunately sparse, with depths given on labels but not bottom types. I have summarized the data I could find. Occurrences in the fossil record are taken from the literature.

References are provided in the Literature Cited for all works and taxa mentioned.

The following abbreviations for institutions and private collections are used in the text.

ANSP—Academy of Natural Sciences of Philadelphia
BM(NH)—British Museum (Natural History)
CAS—California Academy of Sciences, San Francisco
LACM—Los Angeles County Museum of Natural History
MCZ—Museum of Comparative Zoology, Harvard University
MHNG—Muséum d'Histoire Naturelle, Geneva
NMV—Naturhistorisches Museum, Vienna
NSMT—National Science Museum, Tokyo

PRI—Paleontological Research Institution, Ithaca, New
    York
SBMNH—Santa Barbara Museum of Natural History
UAM—University of Alaska Museum, Fairbanks
UCMP—University of California at Berkeley, Museum
    of Paleontology
USGS M.—U.S. Geological Survey, Menlo Park station
    no.
USNM—U.S. National Museum collection, National
    Museum of Natural History, Smithsonian Institution
ZMC—Zoologisk Museum, Copenhagen
ZMO—Zoologisk Museum, Oslo

Baxter Coll.—collection of Rae Baxter, Homer, Alaska
Evans Coll.—collection of Roger A. Evans, Redondo Beach,
    California (cited in DRAPER, 1987)
Skoglund Coll.—collection of Carol C. Skoglund, Phoenix,
    Arizona

A "pair" denotes the two valves of a single individual.
The term "convexity" is used here instead of "thickness"
for the maximum transverse dimension to prevent confu-
sion with the thickness of shell material. The terms for
maximum sizes used here are relative to other members
of the family and are defined as follows: small (0–30 mm),
medium-sized (31–60 mm), and large (61–140 mm).

I have provided coordinates for type localities and key
distributional records. These are given to the nearest min-
ute, except when more precise numbers were already avail-
able on museum labels.

SYSTEMATIC ACCOUNT

Thracioidea Stoliczka, 1870

nom. transl. SCARLATO & STAROBOGATOV,
1979:22, 32, *ex* Thraciidae.

Thraciidae STOLICZKA, 1870:59 [1830]

nom. transl. DALL, 1903:1522, *ex* Thraciinae.

[=Osteodesmatidae DESHAYES, 1830:235[2], as "Famille Les
    Ostéodesmes"; *nom. correct.*, COUTHOUY, 1839:130; re-
    jected under ICZN Art. 40(b). Thraciidae takes pre-
    cedence from 1830 under Art. 40(b)i and Recommen-
    dation 40A.]

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[2] KEEN (1969:850) listed the family "Osteodesmacea Deshayes,
1839," as a synonym of the Thraciidae. This family was intro-
duced by DESHAYES (1830) as a vernacular term, COUTHOUY
(1839) first latinizing it as "Osteodesmacea." Keen termed this
family name "invalid" [presumably meaning unavailable], citing
ICZN Art. 11e (now Art. 11f). However, the name is certainly
available because the generic name upon which it was based was
regarded as valid in 1830 when the family was proposed (Art.
11f(i)1). The family name seems not to have been accepted by
other authors. Because of the synonymization of *Osteodesma*, the
family name can be rejected under *ICZN* Art. 40b, though the
"precedence" of the Thraciidae Stoliczka, 1870, dates from 1830
(Art. 40(b)i and Recommendation 40A).

Thracia BLAINVILLE, 1824:347, *ex* Leach MS[3]

[=*Thracia* SOWERBY, 1823:20, *ex* Leach MS (*nomen nudum*).]
    Type species: *Mya pubescens* PULTENEY, 1799:27–28;
    by monotypy—Europe.
[=*Osteodesma* BLAINVILLE, 1827:659–660, *ex* Deshayes MS.
    Type species: *Anatina myalis* LAMARCK, 1818:464–465;
    by subsequent designation of DALL, 1903:1522; =*Mya
    pubescens* Pulteney, 1799[4].]

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[3] VOKES (1956:763) dated *Thracia* from SOWERBY (1823), and
KEEN (1969:850) followed this. However, VOKES (1967:339; 1980:
211) later changed his mind and regarded Sowerby's use of the
name as being a *nomen nudum*, a conclusion with which I agree.
Sowerby said only that some of his fossils resemble Leach's genus
Thracia, which has an external ligament and which has been
associated with *Anatina* by Lamarck. This is not sufficient in-
formation to recognize any genus; there is no figure attributed
to *Thracia*; and no species are included in it.

The type species of *Thracia* has also been variously interpreted.
BLAINVILLE (1824) included two species—*T. corbuloidea* and *T.
pubescens*. I regard the first of these as being a *nomen nudum* in
this work. The type species is thus fixed by monotypy as *T.
pubescens*. Blainville says of *T. corbuloidea* only that it belongs in
a group of *Thracia* containing "Espèces qui n'ont qu'un cuilleron
sur une valve" [Species which have a resilifer only in one valve].
This does not characterize any *Thracia*, including the species that
Blainville eventually made available under this name in 1827.
Perhaps he was confused by some unusual specimen of *Mya*.
This same information appears in the text of BLAINVILLE's *Man-
uel* (1825), and here he cites a figure. However, his plates were
evidently not published until 1827, only then making the name
available. Some workers have considered *T. corbuloidea* to be
available in 1824, perhaps believing Blainville's description of
the genus to cover this particular species, or perhaps simply not
questioning the adequacy of the one-line description. Some of
these authors also considered BLAINVILLE's (1827) "restriction"
of his concept of *Thracia* to *T. corbuloidea* to constitute a type
designation. However, the modern *ICZN* does not allow this
method of designation. (If *T. corbuloidea* were to be considered
available in 1824, then the type would have been fixed as *T.
pubescens* by the subsequent designation of ANTON, 1838:2).

[4] The genus "*Osteodesma* Blainville, 1825," was placed by KEEN
(1969:850) as an objective synonym of *Thracia*, with the same
type species by original designation. (The "Nouvelles Additions
et Corrections" section of Blainville's *Manuel* is correctly dated
1827, not 1825 as is the rest of the volume.) The path to the
designation of the correct type species of this genus is more
complex than has been assumed, and it has never been clearly
delineated. Blainville did not use the word "type" in the modern
sense, and he employed it in connection with two different nom-
inal species: (a) *Anatina myalis* Lamarck, 1818, on p. 659, and
(b) *Mya "declives"* [misspelling of *declivis*] PENNANT, 1777:79,
on p. 660. Blainville regarded the latter as being an older name
for *Mya pubescens* of Pulteney and of MONTAGU (1803:40–41).
Later authors have regarded Lamarck's *A. myalis* as being a junior
synonym of *Mya pubescens*; "*Mya pubescens* Pulteney," of Mon-
tagu, as being a synonym of *Thracia phaseolina* (LAMARCK, 1818:
492), or of its synonym *Tellina papyracea* POLI, 1791 (p. 43; pl.
15, figs. 14, 18) (*non* GMELIN, 1791:3231); and *Mya declivis*
Pennant as a *nomen dubium*, although perhaps an earlier name
for *Thracia phaseolina*. (I regard Pennant's taxon as being most
probably a junior synonym of *Mya arenaria* LINNAEUS, 1758:
670.) Thus, the type species of *Osteodesma* is not fixed by original
designation, and two more species were also included by Blain-

No other species of *Thracia* is closely similar to the type species of the genus, the large, thick-shelled eastern Atlantic *T. pubescens,* in which the external ligament is partly sunken in a projecting resilifer. The right valve is somewhat more inflated. The pallial sinus is shallow. I have seen one specimen 92 mm in length (SBMNH 25955).

Analysis of the subgeneric names under *Thracia* and the proposal of additional subgenera is a task that awaits a world-wide review of this family. I leave the following two Arctic-Boreal species in *Thracia* s.l. They have a ligament without a projecting resilifer, no evident lithodesma in the adult, and a pustulose external surface,

Thracia devexa Sars, 1878

(Figures 3–5)

Thracia truncata [Brown] var. *devexa* Sars, 1878:
    SARS, 1878: 84–85; figs. 11a, b; LAMY, 1931:296–297;
    SOOT-RYEN, 1941:23–25, 39; pl. 12, figs. 5–10; pl. 4,
    fig. 4; pl. 9, fig. 5 [as *Thracia devexa*]; OCKELMANN,
    1959:156–158; pl. 3, fig. 5; fig. 11; BERNARD, 1979:60–
    61; fig. 105; LUBINSKY, 1980:48, 93, 105; pl. 11, fig. 8;
    map 40; BERNARD, 1983:64 [as *Thracia (Ixartia)*].
Thracia "sp. aff. *T. truncata* Brown (=*T. myopsis* Möller)":
    MACNEIL, 1957:106; pl. 11, figs. 9, 11, 15. [*non* (BROWN,
    1844), *non* MÖLLER, 1842—see synonymy under next
    species.]

Type material and locality: Zoological Museum, Oslo, D.13738, Type 41/2, holotype, pair; length, 28.0 mm; height, 21.8 mm; convexity, 12.9 mm (Figure 3). SOOT-RYEN (1941:24–25) gives reasons for believing that this specimen is Sars' holotype, in spite of the fact that it does not match the 34 mm length given by Sars. Vadsø, Varanger Fjord, northern Norway (70°5′N, 29°47′E).

Description: Medium-sized (length to 40 mm; OCKELMANN, 1959; east Greenland; largest specimen from study area: 26.7 mm; LACM 71-482; Arctic coast of Alaska); thin; right valve slightly more inflated; approximately equilateral; posterior end somewhat produced, truncate; beaks prominent; pallial sinus shallow; surface almost smooth, with irregular growth lines, generally with sparse, well-spaced pustules, especially on posterior slope; periostracum tan; pallial sinus broad, shallow.

Hermaphroditic; planktonic stage either short or lacking (OCKELMANN, 1959:158).

I here illustrate specimens from the Beaufort Sea (Figure 4) and British Columbia (Figure 5).

Distribution and habitat: From northernmost Norway south to Skjerstadfjord (67°13′N), as well as in Novaya

ville in this genus: *Anatina "trapezoidalis"* [misspelling of *trapezoides*] LAMARCK, 1818:464, now regarded as a synonym of *Periploma margaritacea* (LAMARCK, 1801:137), and *Anatina rupicola* LAMARCK, 1818:465, a synonym of *Thracia distorta* (Montagu, 1803). The first subsequent designation I have located is that of DALL (1903): *Anatina myalis* Lamarck. Because this species is most probably a synonym of *Thracia pubescens* (Pulteney), *Osteodesma* is indeed an objective synonym of *Thracia* s.s.

Zemlya, Spitsbergen (Svalbard) (SOOT-RYEN, 1941:39); east Greenland (from 73°16′N to about 60°N) (OCKELMANN, 1959); northern Canada (from 82°N south into Hudson Bay to 54°N) (LUBINSKY, 1980).

On the Arctic Coast of Alaska from off Barter Island, Beaufort Sea (72°15′30″N, 143°39′36″W) (LACM 71-397), to off Pitt Point (71°14′42″N, 152°53′30″W) (SBMNH 35085); in the Bering Sea, from the Navarin Basin (60°26′36″N, 178°17′36″W) (UAM 4709) to SE of the Pribilof Islands (56°13′N, 168°20′W) (UAM 4710). Evidently, isolated populations are on the coast of British Columbia: Shidegate Inlet, Queen Charlotte Islands (53°19′30″N, 131°6′W) (LACM 60-113.1); off southeastern Vancouver Island (49°57′N, 123°38′W) (LACM 69-126.1). The depth range for material from Arctic Alaska through British Columbia is from 7 to 348 m (mean, 80 m). The only bottom type recorded is mud. I have seen 15 lots from the study area.

This species has been recorded in the Nuwok Formation on the Arctic coast of Alaska as "*Thracia* sp. aff. *T. truncata* Brown (=*T. myopsis* Möller)" by MACNEIL (1957). This formation is now regarded as being of late Miocene or early Pliocene age (L. Marincovich, verbal communication, Oct. 1988).

Discussion: I am reporting herein the first records of this uncommon species from the northern Bering Sea and from British Columbia. Future studies may possibly connect these populations.

Thracia myopsis Möller, 1842, *ex* Beck MS

(Figures 6–10)

Thracia myopsis Möller, 1842, *ex* Beck MS:
    MÖLLER, 1842:94 [as "Beck"]; REEVE, 1859:pl. 1, fig.
    5a, b; CONRAD, 1869:54; LAMY, 1931:296–297;
    SOOT-RYEN, 1941:22–23, 38–39; pl. 2, figs. 1–4; pl. 6,
    fig. 4; pl. 8, fig. 4; FILATOVA, 1957:57; OCKELMANN,
    1959:155–157; pl. 3, fig. 4; fig. 11; MACGINITIE, 1959:
    162–163; pl. 23, fig. 9; pl. 24, fig. 4; BERNARD, 1979:
    60–61; fig. 106; LUBINSKY, 1980:48–49, 94; pl. 11, fig.
    11; map 41; SCARLATO, 1981:287–288; fig. 156;
    BERNARD, 1983:64 [as *Thracia (Ixartia)*]; THEROUX &
    WIGLEY, 1983:55, 121; fig. 107; SCARLATO, 1987:234;
    fig. 143.
Thracia couthouyi Stimpson, 1851:
    STIMPSON, 1851a:8; STIMPSON, 1851b:13; CONRAD, 1869:
    54; DALL, 1903:1525 [as a synonym of *T. myopsis*].
"*Thracia truncata* Brown," *auctt., non* Brown, 1844 [Turton, 1822]:
    SARS, 1878:84–85; pl. 6, figs. 10a, b [as "forma typica"].
    [*non* BROWN, 1844:110; pl. 42, fig. 28, which is *Anatina
    truncata* TURTON 1822:46–47, 277; pl. 4, fig. 6, a synonym of *Thracia (Ixartia) distorta* (Montagu, 1803), as
    well as a junior primary homonym of *Anatina truncata*
    LAMARCK, 1818:463.]
Thracia beringi Dall, 1915:
    COOPER, 1894:[12] [*nomen nudum*]; DALL, 1915:442–
    443; I. OLDROYD, 1924:28; pl. 7, fig. 3; I. OLDROYD,
    1925:85; pl. 43, fig. 4; LAMY, 1931:233–234; SCARLATO,
    1981:287 [as a synonym of *T. myopsis*]; BERNARD, 1983:
    64 [as *Thracia (Crassithracia)*].
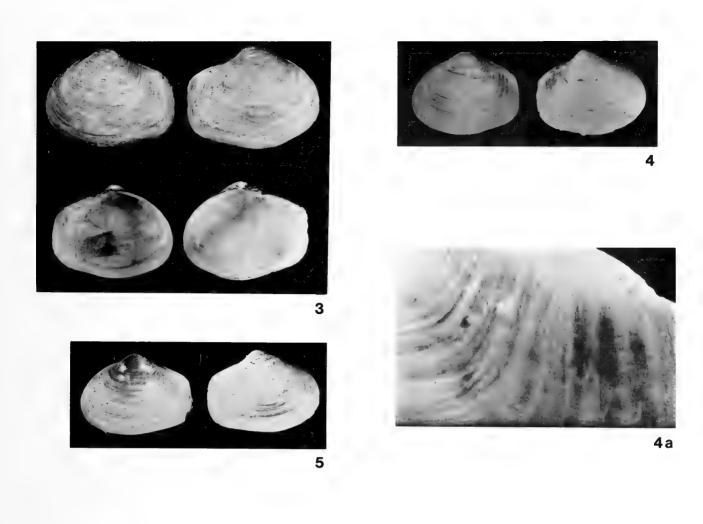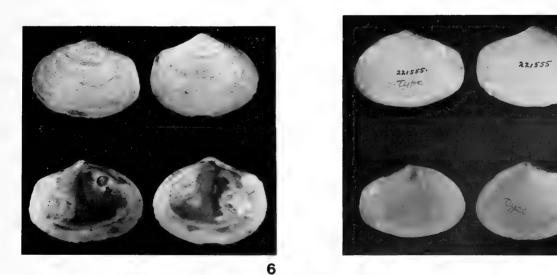
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Explanation of Figures 3 to 7

Figures 3–5. *Thracia* (s.l.) *devexa* Sars. Figure 3: Holotype; ZMO D.13738 (Type 41/2); length, 28.0 mm. Figure 4: SBMNH 35085; off Pitt Point, Beaufort Sea; 40 m; length, 24.4 mm. Figure 4a: Close-up view of posterior slope of left valve. Figure 5: LACM 69-126.1; off SE coast of Vancouver Island, British Columbia; 45 m; length, 25.9 mm.

Figures 6, 7. *Thracia* (s.l.) *myopsis* Möller. Figure 6: **Lectotype (herein)**; ZMC no number; length, 17.7 mm. Figure 7: **Lectotype (herein)** of *T. beringi* Dall; USNM 221555; length, 36.6 mm.

Type material and localities: *T. myopsis*—Zoologisk Museum, Copenhagen (ZMC) no number, **lectotype (herein)**; length, 17.7 mm; height, 13.2 mm; convexity, 7.0 mm (Figure 6); ZMC, paralectotypes, 18 pairs, 17 valves in same lot, plus three other lots; BM(NH) 1843.6.23.204, probable paralectotype; BM(NH) 1988041/1-3, probable paralectotypes, including the specimen figured by Reeve. Greenland; the lot from which a lectotype was selected, the largest available intact pair, has no exact locality. **The type locality is here clarified as Kap Hope, Scoresby Sund** (70°29'N, 22°17'W), where OCKELMANN (1959: 155) obtained the species.

T. couthouyi—Lost in the Chicago fire of 1871 (DALL, 1888:132–133). Massachusetts Bay (approx. 42°20'N, 70°30'W).

T. beringi—USNM 221555, **lectotype (herein)**, pair; length, 33.6 mm; height, 24.6 mm; convexity, 11.6 mm (Figure 7). USNM 859378, paralectotypes, 2 pairs, 6 valves; SBMNH 34449, paralectotype, 2 valves. Kiska Harbor, Kiska Island, Rat Islands Group, Aleutian Islands, Alaska (51°58'N, 177°34'E).

DALL (1915) cited a type locality of the "Commander Islands," but no material from this locality is in the USNM collection. The lot from which a lectotype is selected bears the only number listed in the original description, and it was labeled "type."

Description: Medium-sized (length to 40 mm; USNM 271727; St. Paul Island, Alaska, about 5 mm larger than any reported from elsewhere); average in thickness; right valve larger, more inflated; approximately equilateral; anteroventral margin often somewhat sinuous; posterior end slightly truncate; beaks lower and less prominent than in *Thracia devexa*; pallial sinus shallow; surface with growth lines and dense pustules, particularly on posterior slope and in young specimens.

Specimens from populations in the southern Bering Sea and the Aleutian Islands are often more elongate and thicker-shelled than is *Thracia myopsis* from the Arctic Ocean, and the surface sculpture is often worn off. This was named *T. beringi* by DALL (1915). However, such material intergrades with more typical *T. myopsis,* and the densely pustulose young specimens from these populations are identical to young *T. myopsis* from other areas. SCARLATO (1981) was the first to synonymize these two taxa.

Hermaphroditic, with a short or absent planktonic stage (OCKELMANN, 1959:156).

I have illustrated here specimens from the Bering Sea (Figure 8) and from southeast Alaska (Figure 9), and a juvenile specimen showing a lithodesma (Figure 10).

Distribution and habitat: Circum-Arctic: In the Barents, White, Kara, Laptev, East Siberian, and Chukotsk seas (FILATOVA, 1957); Novaya Zemlya, Spitsbergen (Svalbard), Jan Mayen, and in the eastern Atlantic, south to Bergen, Norway (60°N) (SOOT-RYEN, 1941); Iceland; in eastern Greenland south to Tasissaq, near Angmagssalik (about 65°N) (OCKELMANN, 1959); in the western Atlantic south to off Massachusetts (about 42°N) (THEROUX & WIGLEY, 1983); in west Greenland south to 66°N, and in eastern Canadian Arctic south into southern Hudson Bay to about 54°N (LUBINSKY, 1980)[5]; in the western Pacific south to Zaliv Petra Velikogo (about 43°N) (SCARLATO, 1981).

Throughout the Arctic coast to Alaska, the Bering Sea, and Aleutian Islands, south to Uncluelet, Barkley Sound, Vancouver Island, British Columbia (48°55'N, 125°33'W) (LACM 67-199.1). However, there is a single, small right valve from off Point Loma, California (about 32°33'N, 117°40'W) (USNM 208957)! In the area of study, from the intertidal zone to 183 m (mean, 44 m), with most records from sand and mud bottoms, but some recorded on gravel or among rocks. It is not uncommon; I have seen 101 lots from the study area.

THEROUX & WIGLEY (1983) found this species in the western Atlantic from 95 to 114 m (mean, 105 m) on gravel substrates.

Subgenus (*Cetothrax*) IREDALE, 1949:19

Type species: *Thracia alciope* ANGAS, 1872:611; pl. 42, fig. 6; =*Anatina imperfecta* LAMARCK, 1818:464; by original designation—western Australia.

Shells medium-sized to large. The right valve is larger and more inflated. The ligament is entirely external. It differs from *Thracia (Crassithracia)* in its greater size and inflation and from other subgenera in its lack of conspicuous pustules on the external shell surface. The type species of this genus is more elongate than the eastern Pacific

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[5] LUBINSKY's (1980) map illustrating the distributions of *Thracia myopsis* and *T. septentrionalis* (map 41) does not match the distributions of these taxa given in the text. Evidently, the symbols for the taxa in the map's legend were accidentally reversed.

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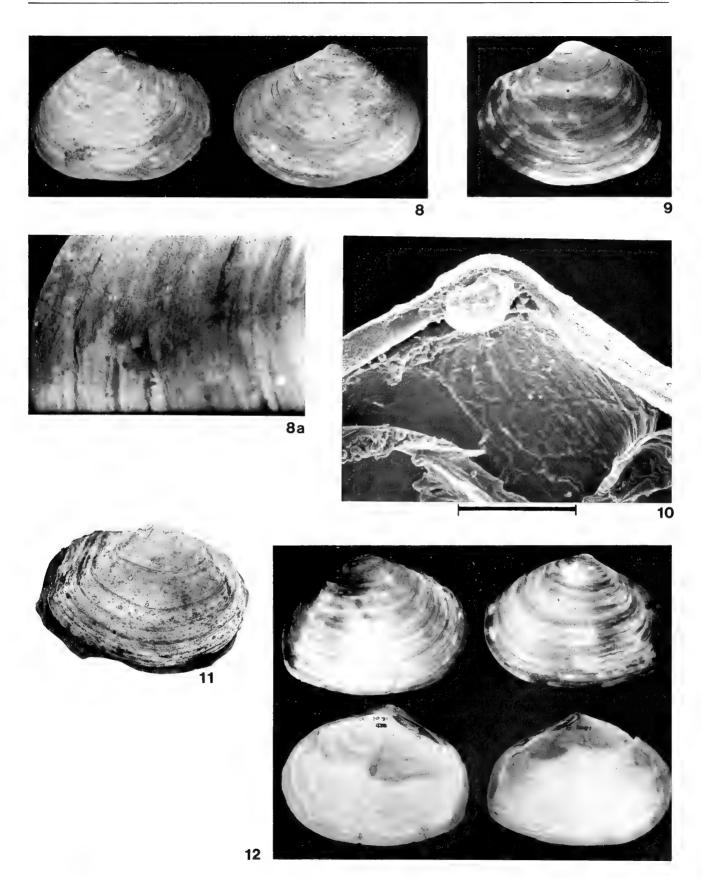
Explanation of Figures 8 to 12

Figures 8–10. *Thracia* (s.l.) *myopsis* Möller. Figure 8: USNM 859368; USGS Loc. M.6283; Bering Sea off Seward Peninsula; length, 29.2 mm. Figure 8a: Close-up of posterior slope of right valve. Figure 9: USNM 220579; Sitka, Alaska; length, 31.0 mm. Figure 10: LACM 73-23; Kachemak Bay, Cook Inlet, Alaska; 9 m; close-up of lithodesma in left valve of a juvenile specimen; scale bar, 200 μm.

Figures 11, 12. *Thracia* (*Cetothrax*) *condoni* Dall. Figure 11: USNM 214143; near Westport, Clatsop Co., Oregon; Pittsburg Bluff Formation; middle Oligocene; length, 46.7 mm (from MOORE, 1976:pl. 16, fig. 1). Figure 12: LACM 57-12.7; Kasitsna Bay, Cook Inlet, Alaska; 46 m; length, 67.0 mm.

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species and has a shorter ligament and a less conspicuous periostracum.

Thracia (Cetothrax) condoni Dall, 1909

(Figures 11, 12)

Thracia condoni Dall, 1909:
    DALL, 1909:135; pl. 19, fig. 5; DALL, 1915:447; B. CLARK, 1918:137; pl. 11, fig. 12; pl. 12, fig. 2; TEGLAND, 1933: 113; pl. 6, fig. 5; WEAVER, 1943:119; pl. 25, fig. 10; pl. 29, fig. 15; DURHAM, 1944:141; pl. 13, fig. 6; ZHIDKOVA *et al.*, 1968:137, 159, 174; pl. 7, fig. 4; pl. 43, fig. 2; HICKMAN, 1969:72–73; pl. 9, figs. 10–14; MOORE, 1976: 54; pl. 16, figs. 1, 3.
Thracia (Crassithracia), n. sp.:
    ROTH, 1979:410–412; pl. 8, fig. 2 [thesis].

Type material & locality: *T. condoni*—USNM 110460, holotype, cast of a right valve, length 60 mm; height 44 mm; convexity, 8 mm (not refigured here). Smith's Quarry, Eugene, Lane Co., Oregon (approx. 44°3'N, 123°4'W); Eugene Formation; early to middle Oligocene; T. Condon & C. A. White.

Description: Large (to 83 mm in length; LACM 60-68.1; Nuka Island, Kenai Peninsula, Alaska); thin-shelled for size; right valve decidedly more inflated; approximately equilateral; posterior end broadly truncate; beaks prominent; pallial sinus short, narrow; surface smooth, with only concentric growth lines; periostracum light tan, darker on posterior slope.

I here figure a specimen from the Oligocene of Oregon (Figure 11) and a Recent specimen from British Columbia (Figure 12).

Distribution and habitat: In the Recent fauna, this species is known from St. Paul Harbor, Kodiak Island (57°44'24"N, 152°25'42"W) (USNM 221313), through the Gulf of Alaska, as far north as Kasitsna Bay, Cook Inlet (59°29'N, 151°36'W) (LACM 57-12.7), south to Clover Point, Victoria, British Columbia (48°24'N, 123°21'W) (CAS 066617). Some of the available material was collected washed up on the shore, with depths recorded for only 5 lots—16 to 81 m (mean, 48 m). The bottom type is recorded for only 1 lot: mud. In the Recent fauna, this rare species is known from only 13 lots representing 10 stations.

Discussion: This species has long been present in collections from Alaska and British Columbia, generally identified as *Thracia challisiana* Dall. Conspecific material is present in late Pliocene and Pleistocene strata of northwestern California and in Pleistocene strata of southwestern Oregon (ROTH, 1979, as "*Thracia (Crassithracia)*, n. sp."). Here I tentatively place this Recent and fossil material into *T. condoni*, which has been reported from a number of formations of Oligocene age in Alaska, Washington, Oregon, and California (MOORE, 1976, reviews these records). It has also been reported from deposits of Miocene age in Siberia (ZHIDKOVA *et al.*, 1968).

Future study may demonstrate whether there are suf-

ficient morphological differences to regard Pliocene-Recent material as a separate species.

Subgenus (*Crassithracia*) SOOT-RYEN, 1941:19

Type species: *Thracia crassa* BECHER, 1886:71, 82; pl. 6, figs. 1, 1a–c; by original designation; =*Thracia septentrionalis crassa* Becher, 1886 (herein) (Figure 13)—Jan Mayen Island, Arctic Atlantic.

This subgenus contains only the following species and its subspecies, *Thracia (C.) septentrionalis crassa*. It is characterized by its smooth shells, without pustules. The shells are often thickened, and in most material the periostracum is shiny. The shells of this subgenus are smaller, thicker, and less inflated than those of *Thracia (Cetothrax)*.

Thracia (Crassithracia) septentrionalis Jeffreys, 1872

(Figures 13–18)

Thracia truncata Mighels & Adams, 1842, *non Anatina truncata* Turton, 1822, a *Thracia*:
    MIGHELS & ADAMS, 1842:38; pl. 4, fig. 1; MIGHELS & ADAMS, 1843:48; CONRAD, 1869:55; CLENCH & TURNER, 1950:353–354; pl. 43, figs. 5–7. [*non Anatina truncata* TURTON, 1822:46, 277; pl. 4, fig. 6, a synonym of *Thracia (Ixartia) distorta* (Montagu, 1803), and a junior primary homonym of *A. truncata* LAMARCK, 1818:463.]
Thracia septentrionalis Jeffreys, 1872 [new name for *Thracia truncata* Mighels & Adams, 1842, *non* "Brown, 1827"[6]]:
    JEFFREYS, 1872:238; SOOT-RYEN, 1941:19–22, 38; pl. 1, figs. 9, 10; pl. 6, fig. 2a, b; pl. 8, fig. 3a–e; OCKELMANN, 1959:153–155; pl. 3, fig. 1; LUBINSKY, 1980:49, 94; map 41; THEROUX & WIGLEY, 1983:55–56, 121, 169; fig. 107; tables 306, 307.
Thracia crassa Becher, 1886:
    BECHER, 1886:71; 82; pl. 6, figs. 1, 1a–c; SOOT-RYEN, 1941:19–22 [as a possible synonym of *T. septentrionalis*].
Macoma truncaria Dall, 1916:
    DALL, 1916a:37 [*nomen nudum*]; DALL, 1916b:414; I. OLDROYD, 1925:177; COAN, 1969:281–282 [as *Thracia (Crassithracia)*]; BERNARD, 1983:64 [as a synonym of *T. beringi* Dall].
?*Thracia seminuda* Scarlato, 1981:
    SCARLATO, 1981:288–289; fig. 157.

Type material and localities: *T. truncata* Mighels & Adams (and *T. septentrionalis*)—MCZ 165595, lectotype (CLENCH & TURNER, 1950), pair; length, 14.5 mm; height, 10.8 mm; convexity, 5.2 mm (Figure 14). Casco Bay, Cumberland Co., Maine (43°45'N, 70°11'W); stomachs of haddock; 1840; 4–5 specimens.

T. crassa—Naturhistorisches Museum, Vienna (NMV) (646) 61967, **lectotype (herein)**, pair; length, 24.1 mm; height, 19.5 mm; convexity, 10.6 mm (Figure 13); NMV, paralectotypes, a smaller pair in the same lot, plus three pairs in NMV 117. Jan Mayen Island, Atlantic-Arctic (70°59'N, 8°40'W); on the beach.

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[6] This name is not present in the first edition of BROWN, published in 1827. Instead, it first appears in the second edition, published in 1844. However, it is not a new species, merely a reassignment of *Anatina truncata* Turton, 1822, to *Thracia*.

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Explanation of Figures 13 to 18
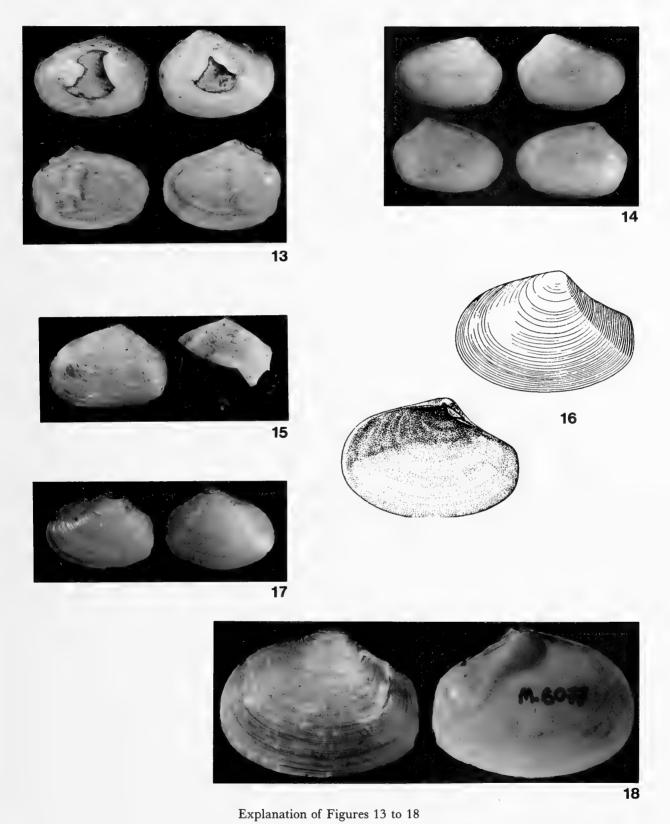
Figure 13. *Thracia (Crassithracia) septentrionalis crassa* Becher. **Lectotype (herein)** of *Thracia crassa;* MNV (646)61967; length, 24.1 mm.

Figures 14–18. *Thracia (Crassithracia) septentrionalis septentrionalis* Jeffreys. Figure 14: Lectotype of *T. truncata* Mighels & Adams (*septentrionalis* Jeffreys); MCZ 165595; length, 14.5 mm. Figure 15: Holotype of *Macoma truncaria* Dall; USNM 210916; length, 15.0 mm. Figure 16: Holotype of *T. seminuda* Scarlato; length, 20.1 mm (from SCARLATO, 1981). Figure 17: CAS 066618; Bristol Bay, Alaska; 49 m; length, 13.0 mm. Figure 18: USNM 859369; USGS Loc. M.6077; Bering Sea, off Seward Peninsula, Alaska; 30 m; length, 28.0 mm.

Macoma truncaria—USNM 210916, holotype, broken pair; length, 15.0 mm; height, 10.5 mm; convexity, approximately 4.5 mm (Figure 15). Between Cape Halkett and Garry "River" [Creek], Arctic coast of Alaska (70°38–48′N, 152°11–27′W).

T. seminuda—Presumably Zoological Institute, Leningrad (Figure 16). Zaliv Petra Velikogo, USSR, Sea of Japan (approx. 42°N, 132°E).

Description: Small (length to 28.0 mm; USNM 859369; off Cape Woolley, Bering Sea, Alaska); oblong; relatively thick shelled; right valve more inflated; longer, sharply rounded anteriorly; posterior end truncate, produced in some; beaks produced; surface smooth, with growth lines only; periostracum light to dark tan, often shiny in Arctic populations, silky in some southern populations; pallial sinus moderately deep, extending past median line; inner ventral margin with vertical striations.

Hermaphroditic, with a short or absent planktonic stage (OCKELMANN, 1959:155).

I have illustrated here two specimens from the Bering Sea (Figures 17, 18).

Distribution and habitat: Probably circum-Arctic: Barents, White, and Kara seas (FILATOVA, 1957); Spitsbergen (Svalbard), Jan Mayen, Iceland (SOOT-RYEN, 1941); in east Greenland south to Tasissaq, near Angmagssalik (about 65°N) (OCKELMANN, 1959); in the western Atlantic south to off Rhode Island (40°N) (THEROUX & WIGLEY, 1983); in west Greenland south to about 64°N; in the Canadian Arctic to northern end of Hudson Bay (about 63°N) (LUBINSKY, 1980) (see footnote 5). If *Thracia seminuda* Scarlato, 1981, is indeed a synonym, this species occurs as far south as Zaliv Petra Velikogo, USSR, in the Sea of Japan (about 43°N).

In the study area, this species is known from six stations on the Arctic coast of Alaska and nine lots from the Bering Sea; south to Popoff Strait, Shumagin Islands (south of the Alaska Peninsula; about 55°15′N, 160°10′W) (USNM 859374). It is recorded from 11 to 69 m (mean, 35 m). The only bottom types recorded are sand and sandy silt. I have examined 16 lots from the study area.

THEROUX & WIGLEY (1983) found this species in the western Atlantic between 23 and 74 m (mean, 54 m), chiefly on sand.

The taxonomic situation here may be more complicated than can be expressed with a single name at the species level, but there is as yet insufficient material to justify recognizing more than one species. However, I here recognize *Thracia septentrionalis crassa* as a subspecies; no material from anywhere else reaches the extreme thickness represented by its type material from Jan Mayen Island. Material from New England, the type locality of *T. septentrionalis,* has a silky periostracum, not shiny as in Arctic specimens. Large adult specimens from the Bering Sea (USNM 859369) (Figure 18) are also silky rather than shiny. *Thracia seminuda* Scarlato, 1981, seems to be of this form as well.

A related fossil species is *Thracia transversa* LEA, 1845 (p. 237; pl. 34, fig. 11), described from the Yorktown Formation at Petersburg, Virginia (types, ANSP 1585), now regarded as being of Pliocene age. As pointed out by GARDNER (1943:44), *T. transversa* is much smaller, none yet found being larger than 10 mm. Additionally, Lea's species is thinner for its size and is longer posteriorly (based on examination of USNM 164645). *Thracia brioni* WARD & BLACKWELDER (1987:161–162; pl. 29, figs. 7–10) has been proposed for material from the late Pliocene and early Pleistocene of North Carolina that is very similar to *T. transversa.*

Subgenus (*Homoeodesma*) FISCHER, 1887:1171

Type species: *Thracia conradi* COUTHOUY, 1839:153–158; pl. 4, fig. 2; by monotypy—eastern Atlantic.

This subgenus is characterized by species with relatively large shells that are inflated anteriorly. They have a ligament that is external in the adult and does not project below the hinge margin in a resilifer. The shell surface is generally very pustulose. In addition to the two eastern Pacific species discussed below, the following six Recent taxa belong in this subgenus:

T. (H.) conradi COUTHOUY, 1839—western Atlantic
T. (H.) convexa WOOD (1815:92; pl. 18, fig. 1)—Europe
T. (H.) corbuloidea BLAINVILLE, 1827:pl. 76, fig. 7 [1825: 565]—Mediterranean
T. (H.) itoi HABE, 1962:143; App., p. 40; pl. 64, fig. 17—Japan
T. (H.) kakumana (YOKOYAMA, 1927:168, 177–178, 182; pl. 47, fig. 14)—Japan
T. (H.) stearnsi DALL, 1886:307; DALL, 1890:275; pl. 13; fig. 2—western Atlantic.

The morphology and behavior of *Thracia (H.) conradi* was discussed by MORSE (1913, 1919) and THOMAS (1967).

Thracia (Homoeodesma) trapezoides Conrad, 1849

(Figures 19, 20)

Thracia trapezoides Conrad, 1849:
CONRAD, 1849c:723; pl. 17, fig. 6a [no 6b present]; CARPENTER, 1857b:367; CARPENTER, 1864b:679 [1872:165] [as a possible synonym of *T. curta*]; DALL, 1909:135; pl. 2, fig. 14; pl. 13, fig. 7; DALL, 1915:447; I. OLDROYD, 1924:27; pl. 7, fig. 2; I. OLDROYD, 1925:84–85; pl. 43, fig. 8; GRANT & GALE, 1931:257–258, 906; pl. 13, fig. 8; MOORE, 1963:84–85; pl. 26, fig. 3; pl. 31, fig. 6; BERNARD, 1983:64.
?"*Thracia ventricosa* Conrad," auctt., non *T. ventricosa* Philippi, 1844:
MEEK, 1864:11 [nomen nudum]. [non PHILIPPI, 1844: 17.]
?*Thracia jacalitosana* Arnold, 1910:
ARNOLD, 1910:68–69; pl. 16, fig. 4; DALL, 1915:447.
Thracia kanakoffi Hertlein & Grant, 1972:
HERTLEIN & GRANT, 1972:338–339; pl. 42, figs. 11, 13–15.

Type material and localities: *T. trapezoides*—USNM 3604, holotype, a cast, mold, and latex impression of mold;

length, 33.8 mm; height, 26.7 mm; convexity, 15.5 mm (Figure 19); paratypes, USNM 561515, 3 specimens. Astoria, Klatsop Co., Oregon (46°10′N, 123°45′W); Astoria Formation; middle Miocene; J. D. Dana; 1841.

T. jacalitosana—USNM 165579, holotype, broken left valve; length, 51 mm; height, 44 mm; convexity, 8 mm [not refigured here]. USGS Loc. 4763, "on Stone Canyon and Coalinga Road," 183 m N of Jacalitos Creek crossing, 22.5 km SW of Coalinga, either Fresno Co. or Monterey Co., California (approx. 36°2′30″N, 120°29′W); "Jacalitos" [Etchegoin] Formation; "Upper Miocene"; R. Arnold and F. Stokes, Jr.

T. kanakoffi—LACM 4839, holotype, pair; length, 81.0 mm; height, 54.2 mm; convexity, 32 mm [not refigured here]. LACM 4840–4881, paratypes. LACM Loc. 291; 0.8 km S of Humphrey Railroad Station, Los Angeles Co., California (34°24′18″N, 118°26′21″W); silt beds exposed in a gully in the center of the S half of Sec. 27, T.4N., R.15W.; Pico Formation; middle Pliocene. The paratypes are from both the Pico Formation, Los Angeles Co., and the San Diego Formation, San Diego Co.

Description: Large (length to 65 mm in Recent material; CAS 066634; Departure Bay, Vancouver Island, British Columbia; and to 132 mm in Pliocene material from San Diego Co., Calif.; HERTLEIN & GRANT, 1972); trapezoidal; approximately equilateral; anterior end inflated, rounded, and often with a slight flexure and radial depression about one-third of distance to posterior end; posterior end produced, truncate, set off by a flexure and, posterior to it, a low ridge; beaks prominent; sculpture of prominent pustules, particularly dense on posterior slope; periostracum dark tan, darker on posterior slope; pallial sinus moderate in size, barely reaching a vertical line from beaks in some specimens.

A Recent specimen from British Columbia is illustrated here (Figure 20).

Distribution and habitat: This eastern Pacific species is known from Wide Bay (S side of Alaska Peninsula), Alaska (57°22′N, 156°11′W) (CAS 066619), throughout the Gulf of Alaska, along the coasts of British Columbia, Washington, Oregon, and California, south to off Isla Cedros, Baja California Norte (28°19′N, 115°10′W) (LACM 71-154). Specimens from populations in the sheltered waters of Puget Sound and the islands of British Columbia attain the largest size; individuals in populations elsewhere are smaller. The species has been recorded from 11 to 199 m (mean, 71 m) on sand and mud bottoms, the latter predominating. I have examined 129 Recent lots.

Thracia trapezoides has been recorded in a number of formations of middle Miocene to Pliocene age from Washington, Oregon, and California. These are not detailed here. It may date from the Oligocene if *T. schencki* B. Clark, 1932, proves to be a synonym (see Discussion).

It is also recorded from early Pleistocene strata in southern California: A. CLARK (1931:opp. p. 30), HOOTS (1931: 120), RODDA (1957:2484), and WOODRING *et al.* (1946: 85).

Discussion: *Thracia kanakoffi* was differentiated by its authors from Recent specimens—*not* from material from the type locality of the species in the Miocene of Oregon—because of its (1) larger size; (2) less steeply sloping posterodorsal margin; (3) the presence of a ridge on the posterodorsal margin of the right valve; and (4) its less developed radial depression anterior to the ridge defining the posterior slope. This Pliocene population clearly attained a larger size than any Recent (or Miocene) material yet observed. However, some Recent material also has a less steeply sloping posterodorsal margin than other specimens, and the posterior slope of the type of *T. trapezoides* and other specimens that have been illustrated from the Miocene of Oregon seem not to have a steeply sloping posterodorsal margin. The degree of production of the posterior end, and the extent of the radial depression setting it off, is also variable in Recent material, as is the strength of posterodorsal ridges in both valves. With this degree of variability, and with the lack of a case for differentiating Pliocene material from specimens from the Miocene of Oregon, I think it unwise to recognize a separate species from the Pliocene of southern California.

It is possible that *Thracia jacalitosana* ARNOLD, 1910 (pp. 68–69; pl. 16, fig. 4), described from the Miocene of central California, is a poorly preserved specimen of *T. trapezoides*. The collection of additional material from its type locality would be required to prove this.

Thracia schencki B. CLARK, 1932 (pp. 801, 808, 845; pl. 15, figs. 2, 3, 5), *ex* Tegland MS, described from the upper Oligocene of Alaska (see also TEGLAND, 1933:112–113, 154; pl. 6, figs. 6–11), is similar to *T. trapezoides* and is either another synonym or ancestral to it. It was differentiated by its author as having a more acute umbonal angle and in lacking a shallow anterior depression. *Thracia kidoensis* KAMADA, 1955 (pp. 11–12, 14; pl. 1, figs. 1, 2a, b), from the Oligocene of Japan, is suspiciously similar to *T. schencki*.

Thracia (Homoeodesma) trapezoides is closely related to the western Atlantic type species of the subgenus, *T. (H.) conradi* Couthouy, 1839. Recent material of that species attains a much larger size (up to 95 mm in material that I have seen), is more inflated, has a straighter posterodorsal margin, a more conspicuous escutcheon, and a light tan periostracum. THEROUX & WIGLEY (1983:55, 120, 169; fig. 106; tables 304, 305) found *T. (H.) conradi* from 34 to 126 m (mean, 70 m), predominantly in silt.

Thracia (Homoeodesma) challisiana Dall, 1915
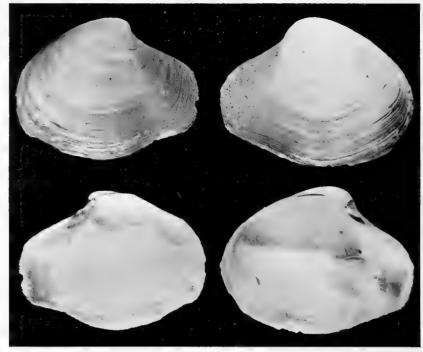
(Figure 21, 21a)

Thracia challisiana Dall, 1915:
    DALL, 1915:443; I. OLDROYD, 1924:27–28, 209; pl. 7, fig. 1; I. OLDROYD, 1925:84; pl. 43, fig. 7; BERNARD, 1983:64 [as *Thracia (Crassithracia)*].

Type material and locality: USNM 272096, holotype, pair; length, 46.2 mm; height, 35.7 mm; convexity, 19.8 mm (Figures 21, 21a). San Juan Island, San Juan Co., Washington (approx. 48°30′N, 123°W); B. M. Challis.

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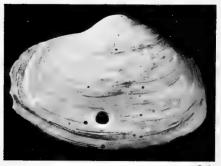
21a

22

Description: Medium-sized (length to 59.5 mm; LACM 140317; Craig, Alaska); oblong; right valve more inflated; anterior end rounded; posterior end decidedly longer in adult, broadly truncate; beaks prominent; surface with fine, conspicuous pustules (Figure 21a); periostracum dark tan; pallial sinus broad, short.

Distribution and habitat: Kasitsna Bay, Cook Inlet (59°21′N, 151°33′58″W) (Baxter Coll.), and Point Woodcock, Montagu Island, Prince William Sound, Alaska (59°54′15″N, 147°48′40″W) (LACM 65-184.1), south to type locality at San Juan Island, Washington (48° 30′N, 123° W); and from off Redondo Beach, Los Angeles Co., California (33°50′N, 118°25′W) (LACM 72-204), to off Isla Guadalupe, Baja California Norte (28°52′N, 118°17′W) (SBMNH 35086). No material is yet known from between these two sets of occurrences. This species is recorded from 29 to 229 m (mean, 72 m), with the deepest records from its southern distribution. I have examined 20 lots.

This species was tentatively reported (as "cf., juv.") from a formation of early Pleistocene age in southern California (VALENTINE, 1961:407).

Discussion: *Thracia (H.) itoi* HABE, 1962 (pp. 143; App. 40; pl. 64, fig. 17) is a closely related Japanese species, described from Onagawa Bya, Miyagi Prefecture, with similar densely pustulose sculpture (Figure 22). It is more elongate, and it may attain a larger size, the type measuring 64.5 mm in length. The ligament is proportionately shorter and extends somewhat ventrally on a resilifer.

In the area of overlap with *Thracia myopsis,* young specimens of this species can be distinguished by their more elongate ligament, straighter ventral margin, more pustulose sculpture, and less prominent beaks.

Subgenus (*Ixartia*) LEACH, 1852:272

Type species: *Mya distorta* MONTAGU, 1803:42–44; pl. 1, fig. 1; by monotypy—eastern Atlantic.
[=*Rupicola* FLEURIAU-BELLEVUE, 1802a:348, 354; 1802b: 106–107; genus without named species (only species name present is a vernacular). *Non Rupicola* BRISSON, 1760, vol. 4:437. Original list and subsequent designation by RÉCLUZ, 1846:409, 424: *Anatina rupicola* LAMARCK, 1818:465; =*Mya distorta* Montagu, 1803.]
[=*Rupicilla* SCHAUFUSS, 1869:18, presumably a new name for *Rupicola* Fleuriau-Bellevue.]

[?=*Pelopia* H. ADAMS, 1868:16–17, *non* MEIGEN, 1800:18. Type species: *P. brevifrons* H. ADAMS, 1868:17; pl. 4, figs. 16, 16a, by monotypy—locality unknown.]

Rupicola Fleuriau-Bellevue, 1802, was the first generic unit proposed in the Thraciidae, but it is a homonym. *Pelopia* H. Adams, 1868, also a junior homonym, was synonymized by KEEN (1969:850) with *Ixartia.* However, it was described as having a large lithodesma, suggesting that it does not belong here. Its type specimen should be reexamined, and a replacement name provided if it proves to be a useful generic unit.

Species in this subgenus are nestlers, although some taxa, such as the eastern Pacific *Thracia curta,* may also be free-living. Species may be distorted by their nestling habitat, and even the free-living forms show significant variability in shell form. Members of this subgenus have a projecting resilifer and sculpture of conspicuous pustules. In addition to the two eastern Pacific species, the following taxa appear to belong in this subgenus:

T. (I.) morrisoni PETIT, 1964:157–159; figs. 1–6—southeastern USA [synonym: *T. corbuloidea* Blainville, *auctt., non* Blainville, 1827]

T. (?I.) brevifrons (H. Adams, 1868)—locality unknown

T. (I.) cuneolus REEVE, 1859:pl. 1, fig. 2—southern Japan and the Philippine Islands

T. (I.) distorta (Montagu, 1803)—eastern Atlantic [synonyms (partial list): *Anatina rupicola* LAMARCK, 1818:465; *Anatina truncata* TURTON, 1822:46–47, 277; pl. 4, fig. 6 (*non* LAMARCK, 1818:463); *Thracia brevis* DESHAYES, 1846:297; pl. 81, figs. 4–6; *Thracia concentrica* RÉCLUZ, 1853:122, 129–131, *ex* Fleuriau-Bellevue MS]

T. (I.) rudis REEVE, 1859:pl. 3, fig. 21—Malacca [Strait]

T. (I.) similis COUTHOUY, 1839:150–152; pl. 4, fig. 3—southern Caribbean [synonyms: *T. rugosa* ORBIGNY, 1846: 519, *ex* Conrad MS; *T. distorta* Montagu, *auctt., non* Montagu, 1803]

T. (I.) n. sp.?—Argentina [ANSP 103366, 343169; LACM 78-92].

Thracia (Ixartia) curta Conrad, 1837

(Figures 23–27)

Thracia curta Conrad, 1837:
CONRAD, 1837:248; pl. 19, fig. 8; CARPENTER, 1857a: 210; CARPENTER, 1857b:194, 300, 349; CARPENTER, 1864b:540, ?602, 638 [1872:26, ?88, 124]; CONRAD, 1869:54; DALL, 1915:442; I. OLDROYD, 1924:27, 209;
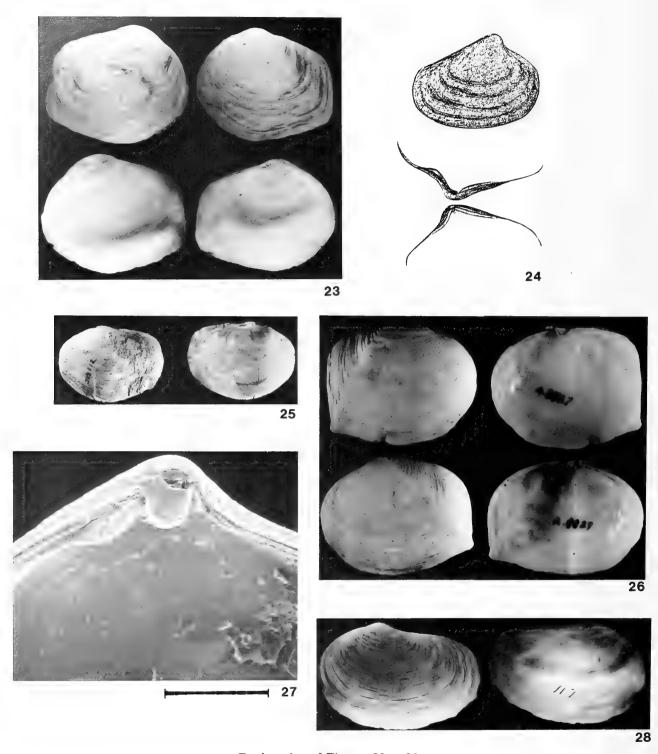
←

Explanation of Figures 19 to 22

Figures 19, 20. *Thracia (Homoeodesma) trapezoides* Conrad. Figure 19: Holotype of *T. trapezoides*; USNM 3604; length, 33.8 mm. Figure 20: LACM 62-120.1; Howe Sound, British Columbia; 46 m; length, 63.7 mm.

Figure 21. *Thracia (Homoeodesma) challisiana* Dall. Holotype; USNM 272096; length, 46.2 mm. Figure 21a: Close-up of posterior slope of right valve.

Figure 22. *Thracia (Homoeodesma) itoi* Habe. Holotype; NSMT 53347; Onagawa Bay, Miyagi Pref., Japan; length, 64.5 mm.

Explanation of Figures 23 to 28

Figures 23–27. *Thracia (Ixartia) curta* Conrad. Figure 23: Holotype; BM(NH) 1861.5.20; length, 27.1 mm. Figure 24: Holotype of *Lepton clementinum*; length, 0.9 mm (Carpenter's figure, from BRANN, 1966:pl. 14, fig. 157). Figure 25: Holotype of *T. quentinensis* Dall; USNM 333112; length, 46.0 mm. Figure 26: LACM 140425; Bahía San Carlos, Sonora, Mexico; length, 37.0 mm. Figure 27: LACM 71-170; Punta Thurloe, Baja California Sur; 16 m; close-up of right valve showing lithodesma and anterior lateral tooth; scale bar, 250 μm.

Figure 28. *Thracia (Ixartia) anconensis* Olsson. Holotype; ANSP 218955; length, 34.0 mm.

pl. 7, fig. 4; I. OLDROYD, 1925:83; pl. 43, fig. 6; GRANT
& GALE, 1931:258–259; HERTLEIN & STRONG, 1946:
95; HERTLEIN, 1957: 63, 74; pl. 13, figs. 7, 8; KEEN,
1958:230–231; fig. 589; KEEN, 1966a:171; KEEN, 1971:
295; fig. 760; BERNARD, 1983:64 [as *Thracia (Ixartia)*].
?Lepton clementinum Carpenter, 1857:
    CARPENTER, 1857b:248, 308 [*nomen nudum*]; CAR-
    PENTER, 1857c:110–111; KEEN, 1958:107; BRANN, 1966:
    39; pl. 14, fig. 157; KEEN, 1968:396; KEEN, 1971:140–
    142; fig. 326 [as *?Mysella*]; BERNARD, 1983:32.
Thracia quentinensis Dall, 1921:
    DALL, 1921:21; DALL, 1925:28; pl. 11, fig. 1; GRANT
    & GALE, 1931:250.

Type material and localities: *T. curta*—BM(NH)
1861.5.20, holotype, pair; length, 27.1 mm; height, 22.8
mm; convexity, 17.3 mm (Figure 23). Conrad was mis-
taken in calling this a single valve. Santa Barbara, Santa
Barbara Co., California (about 34°24′N, 119°43′W); T.
Nuttall; spring 1836 (GRAUSTEIN, 1967:313–315).

L. clementinum—Lost (KEEN, 1968). Carpenter said he
had a single valve, but his drawings, published by BRANN
(1966), show both valves (Figure 24); perhaps he guessed
what the hinge of the left valve would have been like? In
any event, Carpenter had damaged the specimen, and it
is now missing from its BM(NH) mount. The original
specimen measured 0.9 mm in length, 0.6 mm in height,
and 0.5 mm in convexity (a pair might have been about
1.0 mm in convexity). Mazatlán, Sinaloa, Mexico (23°12′N,
106°25′W); off *Spondylus*; F. Reigen.

T. quentinensis—USNM 333112, holotype, left valve;
length, 46.0 mm; height, 33.3 mm; convexity, 11.7 mm
(Figure 25). Bahía San Quintín, Baja California Norte
(about 30°26′N, 115°56′W); Pleistocene; C. R. Orcutt,
Nov. 1888.

Description: Medium-sized (length to 53.4 mm; Evans
Coll.; Bahía San Carlos, Sonora, Mexico; cited in DRAPER,
1987:39; 53 mm; Skoglund Coll.; Puerto Lobos, Sonora,
Mexico); shells often thickened; oval to trigonal, depending
on habitat; right valve generally more inflated; rounded
anteriorly; slightly to decidedly longer posteriorly; poste-
rior end moderately to decidedly truncate, depending on
habitat; posterior end sometimes sharply separated from
central slope by a radial ridge; valves sometimes twisted
to the right posteriorly; ventral margin sometimes sinuous;
beaks low; surface with pustules, particularly prominent
on posterior slope, and concentric growth lines; pallial
sinus broad, shallow; shell sometimes greenish internally.

I have here illustrated a specimen from Sonora, Mexico
(Figure 26).

Distribution and habitat: O'Neal Islet, San Juan Islands,
Washington (48°36′N, 123°5′W) (CAS 066632); off S end
of Vancouver Island, British Columbia (48°32′N, 125°2′W)
(LACM 64-130.1); Monterey, California (36°38′N,
121°56′W) (LACM 72-12; CAS 066620–066622, 066631;
UCMP 239; USNM 5233, 74229, 742163), southward in
California and Baja California, throughout the Gulf of
California, south to Punta Quepos, Puntarenas Prov., Cos-

ta Rica (9°24′43″N, 84°9′41″W) (LACM 72-58); from the
intertidal zone to 48 m (mean, 12.6 m—but some lots
without depth data were probably obtained from the in-
tertidal zone, so this mean may be too deep). It nestles in
rock crevices and empty pholad holes, but can also be found
free-living on various bottom types. This is the most com-
mon thraciid in collections from the eastern Pacific; I have
seen 132 lots, including the type specimens.

Published records of this species from Alaska were based
on specimens of other species, including *Thracia myopsis,
T. trapezoides,* and *T. challisiana.*

This species has been reported from strata of Pleistocene
age from Long Beach (T. OLDROYD, 1914:82) and San
Nicolas Island (VEDDER & NORRIS, 1963:46), in Califor-
nia; Bahía San Quintín, Baja California Norte (DALL,
1921, as "*T. quentinensis*"); and Bahía Santa Inéz, Baja
California Sur (HERTLEIN, 1957).

Discussion: This species displays a variety of forms, de-
pending on habitat.

As with most, if not all, species of *Thracia,* juvenile
specimens have a proportionally large lithodesma, which
only later develops a predominantly external ligament. (In
the case of adult *T. curta* and a number of other species,
the external ligament is partly seated in a projecting re-
silifer.) The lithodesma is never lost but remains tiny and
hard to detect. However, young specimens can be mistaken
for members of unrelated groups. For example, Carpen-
ter's tiny *Lepton clementinum,* described from Mazatlán,
Mexico, was probably a juvenile thraciid, and not, as KEEN
(1971) and BERNARD (1983) thought, a *Mysella,* some
species of which have a lithodesma (W. CLARK, 1855:145–
146). Carpenter's specimen most likely was a young *T.
curta,* the distribution of which includes Mazatlán (as CAS
066633; SBMNH 35087). I here illustrate a young spec-
imen of *T. curta* (Figure 27), but not one as small as the
type of *Lepton clementinum.* It also shows an anterior lat-
eral tooth, present in right valves of juveniles, that dis-
appears with growth.

Thracia quentinensis Dall is a typical free-living form
of *T. curta.* Live-collected specimens similar to material
from the Pleistocene of Bahía San Quintín have been found
throughout the distribution of *T. curta.* The type specimen
of *T. quentinensis* is somewhat unusual in that it is an
inflated left valve, whereas in most *T. curta* the right valve
is the more inflated. However, in other material from the
type locality of *T. quentinensis,* the right valve is more
inflated (SBMNH 35105). In the Panamic province, small
specimens of *T. curta* may be distinguished from similar-
sized specimens of *T. squamosa* by the former's more pro-
jecting resilifer, denser pattern of pustules, and longer
posterior end.

Thracia (Ixartia) anconensis Olsson, 1961

(Figure 28)

Thracia anconensis Olsson, 1961:
    OLSSON, 1961:458–459; pl. 83, figs. 4, 4a; KEEN, 1971:
    295–296; fig. 758; BERNARD, 1983:64.

Type material and locality: ANSP 218955, holotype, left valve; length, 34.0 mm; height, 22.0 mm; thickness, 6.3 mm (Figure 28). Punta Ancon, Santa Elena Peninsula, Guayas Prov., Ecuador (2°20'S, 80°53'30"W), presumably washed up on the beach; A. A. Olsson, 1958.

Description: Medium-sized (to 34 mm; holotype); similar to the free-living form of *Thracia curta*; anterior end rounded; posterior end longer than that in *T. curta*, only slightly truncate; ventral margin evenly curved, unlike the sinuous margin of most *T. curta*.

As more material comes to light, perhaps from between the most southerly known station for *Thracia curta* in Costa Rica and Ecuador, the relationship between the two will have to be reexamined.

Distribution and habitat: Known only from the holotype.

Subgenus (*Odoncineta*) Costa, 1829:xiv, cxxxi; pl. 2, figs. 1–4

Type species: *Tellina papyracea* POLI, 1791:43; pl. 14, figs. 14–18; by monotypy; *non Tellina papyracea* GMELIN, 1791:3231; =*Amphidesma phaseolina* LAMARCK, 1818: 492[7]—Europe.

[?=*Eximiothracia* IREDALE, 1924:181, 199. Type species: *Thracia speciosa* ANGAS, 1869:48–49; pl. 2, fig. 12; by original designation—Australia.]

The name of this subgenus has been subject to many misspellings and unjustified emendations, too many to list here. Species of this subgenus are elongate and thin-shelled, with a ligament that is chiefly external in the adult. A lithodesma is evident in the adult and ranges from small to fairly conspicuous. The shell surface is covered with fine pustules. *Eximiothracia* differs from *Odoncineta* only in the presence of iridescence on the inside of the valves.

There are three European species, which were reviewed by SOOT-RYEN (1941) and ALLEN (1961):

T. (O.) gracilis JEFFREYS, 1865:37 [synonym: *T. rectangularis* SOOT-RYEN, 1941:28–29; pl. 3, figs. 11–14; pl. 7, fig. 3; pl. 10, fig. 11]

T. (O.) phaseolina (Lamarck, 1818) [synonym: *Tellina papyracea* Poli, 1791, *non* Gmelin, 1791; there are a number of additional synonyms]

T. (O.) villosiuscula (MACGILLIVRAY, 1827:370–371, 410; pl. 1, figs. 10, 11) [synonym: *Anatina intermedia* W. CLARK, 1855:141–142].

There appears to be a new species of this subgenus in the western Atlantic, including material reported from Yucatan by DALL (1886:308) as "*Thracia phaseolina* Kiener" (USNM 64062) (see Discussion under *T. (O.) bereniceae*).

There is one probable Australian member of this sub-

genus (cited above). Two Asian species appear to belong here as well:

T. (O) concinna (REEVE, 1859:pl. 3, fig. 17, *ex* Gould MS)— Japan & Philippine Islands

T. (O.) koyamai (HABE, 1981:187–188; pl. 3, fig. 4)—Japan.

Thracia (Odoncineta) squamosa Carpenter, 1856

(Figures 29, 30)

Thracia squamosa Carpenter, 1856:
CARPENTER, 1856:229–230; CARPENTER, 1857b:287, 300, 366; REEVE, 1859:pl. 3, fig. 16; CARPENTER, 1864b: 619 [1872:105]; CONRAD, 1869:55; DALL, 1915:444; LAMY, 1931:233; KEEN, 1958:230–231; fig. 590; PALMER, 1963:320, 393; pl. 63, figs. 16, 17; KEEN, 1971: 295–296; fig. 761; BERNARD, 1983:64.

Type material and locality: BM(NH) 1966570, holotype, partly broken pair; length, 27.9 mm; height, 16.0 mm; convexity (of left valve), 4.1 mm (pair would have been about 8.2 mm) (Figure 29). Mazatlán, Sinaloa, Mexico (23°12'N, 104°20'W); C. Shipley.

Description: Medium-sized (length to 36 mm; SBMNH 35088; Isla Gibraleón, Archipiélago de las Perlas, Panama); thin; approximately equivalve; somewhat longer, sharply round anteriorly; truncate posteriorly; posterior slope set off by a low ridge; surface with conspicuous pustules, most prominent on posterior slope; hinge plate unbroken under umbones; lithodesma small; periostracum tan; pallial line broad, stopping just short of vertical line from beaks.

Distribution and habitat: Bahía Magdalena, Baja California Sur (24°38'N, 112°19'W) (CAS 066623), throughout the Gulf of California, south to Isla Gibraleón, Archipiélago de las Perlas, Panama (8°31'N, 79°3'W) (SBMNH 35088), and Isla Ranchería, Golfo de Chiriqui, Panama (7°37'N, 81°43'W) (Skoglund Coll.). This species has been recorded from the intertidal zone to 61 m (mean, 19 m); there are four records from sand, one from mud. I have examined 32 lots, including the type specimen.
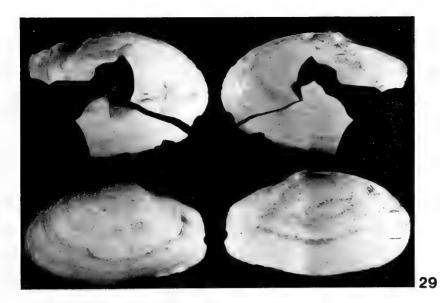
I have illustrated here a specimen from the southern Gulf of California (Figure 30).
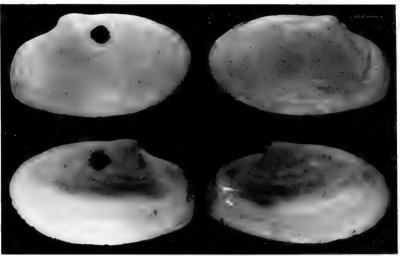
Discussion: Young specimens of *Thracia squamosa* in the Panamic province can be distinguished from specimens of *T. curta* of similar size by their shorter posterior end, less projecting resilifer, and sparser pattern of pustules. (See next species for additional comparative comments.)
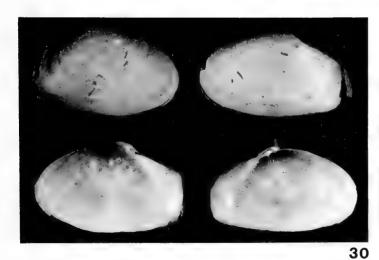
Thracia (Odoncineta) bereniceae Coan, sp. nov.

(Figure 31, 31a)

Type material and locality: SBMNH 35089, holotype; length, 17.5 mm; height, 10.1 mm; convexity, 5.0 mm (Figure 31). SBMNH 35090, paratypes, 5 pairs and 1 valve. One of these paratypes will be placed in the USNM, CAS, and ANSP. Bahía Cholla, Sonora, Mexico (31°21'N, 113°37'W); dead on sand bars at low tide; C. Skoglund; 26 Feb. 1967.

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[7] GMELIN (1791) was published prior to 14 May (HOPKINSON, 1908). It is not known when POLI (1791) was published, so it must be dated as 31 Dec. (*ICZN* Art. 21(c)(ii)). Therefore, *Tellina papyracea* Poli is a junior homonym of *T. papyracea* Gmelin, and we must use the next available name for this species, *Amphidesma phaseolina* Lamarck, 1818.

29

31

30

31a
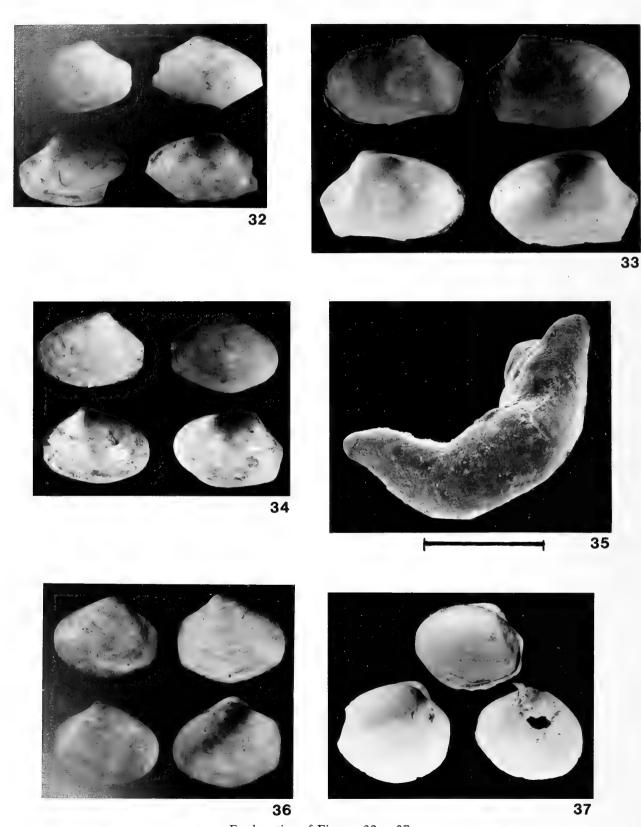
Explanation of Figures 29 to 31

Figures 29, 30. *Thracia (Odoncineta) squamosa* Carpenter. Figure 29: Holotype; BM(NH) 1966570; length, 27.9 mm. Figure 30: SBMNH 35103; La Paz, Baja Calif. Sur; intertidal zone; length, 21.7 mm.

Figure 31. *Thracia (Odoncineta)* **bereniceae** Coan, sp. nov. Holotype; SBMNH 35089; length, 17.5 mm. Figure 31a: Close-up of lithodesma, left valve.

Explanation of Figures 32 to 37

Figures 32, 33. *Asthenothaerus* (*A.*) *villosior* Carpenter. Figure 32: Holotype; USNM 16292; length, 9.6 mm. Figure 33: SBMNH 35104; Puerto San Carlos, Bahía Magdalena, Baja California Sur; 4 m; length, 11.8 mm.

SBMNH 35106, paratypes, 3 pairs; Skoglund Coll., paratypes, 3 pairs. Bahía Cholla, Sonora, Mexico; dead on sand bars at low tide; M. Johnson, April 1967.

Description: Small (length to 25.0 mm; a paratype), thin; right valve slightly more inflated; anterior end much longer, sharply rounded; posterior end narrowly truncate; surface very finely granular, not punctate; pallial sinus long and narrow, reaching past beaks; hinge with an external ligament; hinge plate with a slot for a conspicuous lithodesma that reaches the shell wall of each valve underneath the umbones.

Distribution and habitat: As yet known from only 7 lots, the following 5 in addition to the type lots:

LACM 73-3—Bahía del Coyote, Bahía Concepción, Baja California Norte; 9–27 m—1 valve
LACM 73-122—Isla Blanca, Bahía Concepción, Baja California Norte; 11–18 m—3 valves
LACM 66-30—La Paz, Baja California Sur; 37–55 m; mud—2 valves
SBMNH 35091—Gulf of Tehuantepec, Oaxaca, Mexico; 9–27 m; sand—1 valve
SBMNH 35092—Bahía Ballena, Gulf of Nicoya, Costa Rica; 15–21 m—1 pair.

Thus, the species is known from Bahía Cholla, Sonora, Mexico (31°21′N, 113°37′W), to Bahía Ballena, Gulf of Nicoya, Costa Rica (9°44′N, 85°W); from the intertidal zone to 46 m (mean, 20 m); both sand and mud bottoms.

Discussion: This species differs from *Thracia* (*O.*) *squamosa* in having a large lithodesma (Figure 31a), more elongate dimensions, a longer anterior end, a narrower posterior end that is generally more rounded in adults, smoother surface, and more elongate pallial sinus.

This new species is similar to an as yet undescribed western Atlantic species known from 9 lots: ANSP 175658 and USNM 83162 from Florida; ANSP 298819, 298928, and 329526 from the Bahamas; USNM 64062 from Yucatan Strait; and AMNH 191043 and 191075 and ANSP 249402 from the Virgin Islands. It differs from the new species in having stronger concentric sculpture and a more truncate posterior end, and in being more inflated.

The species name is in recognition of the help my mother, Berenice Coan, has given me over the years in my work in malacology, particularly with proofreading.

Asthenothaerus Carpenter, 1864a:311

Type species: *A. villosior* Carpenter, 1864; by monotypy—eastern Pacific.

Species of *Asthenothaerus* differ from *Thracia* in their complete lack of an external ligament. The hinge is thin, and there is a butterfly-shaped lithodesma (Figure 35). (The anatomical discussion and figure of *Asthenothaerus*

in Pelseneer (1911) was probably based on something else—see Introduction herein.)

Subgenus (*Asthenothaerus*) s.s.

Shells small; lithodesma small.

In addition to the two eastern Pacific species, there is one in the western Atlantic:

A. (*A.*) *hemphillii* Dall, 1886:308–309; Dall, 1902:510; pl. 31, fig. 9—Florida [synonym: *A. balesi* Rehder, 1943a: 189; pl. 19, figs. 13, 14].

Two Japanese species have also been placed in this genus and probably belong in this subgenus:

A. *sematana* (Yokoyama, 1922:173; pl. 14, figs. 17, 18)
A. *isaotakii* Okutani, 1964:83–85; text fig. 6.

Asthenothaerus (*A.*) *villosior* Carpenter, 1864

(Figures 32, 33)

Asthenothaerus villosior Carpenter, 1864:
CARPENTER, 1864a:311 [1872:209]; CARPENTER, 1864b: 618 [1872:104]; CONRAD, 1869:56; DALL, 1915:446; I. OLDROYD, 1925:86–87; SCHENCK, 1945:516; pl. 66, figs. 11, 12; KEEN, 1958:230–231; fig. 591; PALMER, 1958: 75–76, 329; pl. 4, figs. 5–9; PALMER, 1963:320–321 [as *A. "villosier"*]; KEEN, 1971:296–297; fig. 762; BERNARD, 1983:64.

Type material and locality: USNM 16292, holotype, broken pair; length, 9.6 mm (may have been closer to 10 mm); height, 6.4 mm; convexity, 3.8 mm (Figure 32). Cabo San Lucas, Baja California Sur (22°52′N, 109°54′W); J. Xantus.

Description: Small (to 10 mm; holotype), elongate; right valve somewhat more inflated; anterior end longer, sharply rounded; posterior end produced, truncate; surface with very fine granulations and conspicuous concentric undulations that become more evident toward ventral margin; periostracum light tan; pallial sinus elongate, reaching well past beaks.

Distribution and habitat: E side of Isla de Cedros, Baja California Norte (28°13′N, 115°9′30″W) (LACM 71-94), into and throughout the Gulf of California, south to Punta Quepos, Puntarenas Prov., Costa Rica (9°22′43″N, 84°9′41″W) (LACM 72-58), from the intertidal zone to 73 m (mean, 19 m); recorded on a variety of substrates, mostly sand and rocks, suggesting that the species lives in the sand matrix among rubble. I have examined 41 lots including the type specimen.

Here I illustrate a specimen from Baja California (Figure 33).

Discussion: The largest specimens have been obtained from the southern part of the Gulf of California, material

← Figures 34, 35. *Asthenothaerus* (*A.*) *diegensis* (Dall). Figure 34: **Lectotype (herein)** of *Thracia diegensis*; USNM 73604; length, 8.4 mm. Figure 35: LACM 59890; San Pedro, California; lithodesma; scale bar, 250 µm.

Figures 36, 37. *Asthenothaerus* (**Skoglundia**) *colpoica* (Dall). Figure 36: Holotype of *Thracia colpoica*; USNM 73639; length, 17.3 mm. Figure 37: CAS 066627; Guaymas, Sonora, Mexico; closed pair; length, 23.0 mm; open pair, showing lithodesma; length, 23.7 mm.

from the outer coast of Baja California and from Costa Rica being smaller. Specimens from Costa Rica have heavier concentric ribs than material from elsewhere.

KEEN (1958) synonymized *Asthenothaerus diegensis* with this species, but it is distinct, being more inflated and less produced posteriorly.

Juvenile specimens of this species are difficult to distinguish from those of *Thracia* (*Ixartia*) *curta*.

Asthenothaerus (*A.*) *diegensis* (Dall, 1915)

(Figures 34, 35)

Thracia diegensis Dall, 1915:
  DALL, 1915:443; I. OLDROYD, 1925:85; KEEN, 1958: 231 [as a synonym of *A. villosior*]; KEEN, 1971:297 [as a synonym of *A. villosior*]; BERNARD, 1983:64 [as a synonym of *A. villosior*].
Asthenothaerus villosior Carpenter, *auctt.*, *non* Carpenter, 1864: WILLIAMSON, 1905:121. [*non* CARPENTER, 1864a:311.]

Type material and locality: USNM 73604, **lectotype (herein)**; length, 8.4 mm; height, 6.5 mm; convexity, 3.8 mm (Figure 34). USNM 859379, paralectotypes, 4 pairs, 15 valves (most probably forming pairs), plus a few fragments. San Diego Bay, San Diego Co., California (32°40'N, 117°10'W); 2–9 m; sandy mud.

Description: Small (length to 11.0 mm; Bahía Todos Santos, Baja California Norte; LACM 64301), oval; right valve more inflated; anterior end longer, inflated, rounded; posterior end slightly produced, truncate; periostracum tan, most evident near ventral margin; surface with very fine granules, most evident near ventral margin; pallial sinus just reaching ventral line from beaks.

Distribution and habitat: San Pedro, Los Angeles Co., California (33°44'42"N, 118°11'24"W) (CAS 066624), to Bahía Magdalena, Baja California Sur (24°38'N, 112°9'W) (USNM 217825; CAS 066625); Bahía de Los Angeles, Baja California Norte (28°55'N, 113°31'W) (CAS 066626; Skoglund Coll.); Soladita Cove, Guaymas, Sonora (27°54'N, 110°58'W) (LACM 68-27; juveniles, probably this species). There is a single pair labeled "50 m off Newport, Oregon" (about 45°N) (LACM 140426), a locality I doubt because of the lack of any specimens of this shallow-water species from between Oregon and southern California; this may be the result of a transcription error for Newport, California, where the species has been obtained (CAS 018071). Recorded from the intertidal zone to 119 m (mean, 23 m) on mud and sand bottoms. Not uncommon; I have examined 58 lots, including the types.

Discussion: This species is closest to the western Atlantic *Asthenothaerus* (*A.*) *hemphillii* Dall, which attains a larger size and is less flattened.

(*Skoglundia*) Coan, subgen. nov.

Type species: *Thracia colpoica* Dall, 1915—eastern Pacific.

Extremely thin and easily damaged, and probably as a result extremely rare in collections. It is oval in outline,

and the right valve is decidedly more inflated than the left. The ligament is internal, supported by a large, butterfly-shaped lithodesma that abuts each valve under the umbones.

This subgenus differs from *Asthenothaerus* (*Asthenothaerus*) in being much larger and in having a still more conspicuous lithodesma. It differs from *Bushia* in having very thin shells without concentric sculpture and in possessing a butterfly-shaped lithodesma, not a bar-shaped one.

A similar lithodesma is present in "*Thracia*" *rushi* PILSBRY (1897:292–293; pl. 7, fig. 30) from Uruguay and Argentina. This species, which has a small segment of external ligament, has a thicker, more evenly oval shell. It was placed in *Asthenothaerus* by CARCELLES (1947:3–4).

The new subgenus is named for Carol C. Skoglund of Phoenix, Arizona, who generously contributed material for this and other studies.

Asthenothaerus (*Skoglundia*) *colpoica* (Dall, 1915)

(Figures 36, 37)

Thracia colpoica Dall, 1915:
  DALL, 1915:443–444; KEEN, 1958:230–231; fig. 588; OLSSON, 1961:458, 556; pl. 83, figs. 7, 7a; KEEN, 1971: 295–296; fig. 759; BERNARD, 1983:64.

Type material and locality: USNM 73639, holotype, pair; length, 17.3 mm; height, 14.5 mm; convexity, 8.0 mm (Figure 36). "Gulf of California," **here clarified as being Guaymas, Sonora, Mexico** (27°55'N, 110°53'W), where the species has been collected (CAS 066627).

Description: Small (length to 23.7 mm; CAS 066627; Guaymas, Sonora), very thin-shelled, rounded; right valve larger, more inflated; anterior end much longer, rounded; posterior end truncate; posterior slope set off by a low ridge; escutcheon present, more evident in right valve; surface with conspicuous growth lines; no pustules evident; periostracum thin, light tan on posterior slope; pallial sinus broad, short; internal ligament with a large, butterfly-shaped lithodesma.

I have illustrated two complete specimens from Guaymas, one showing the lithodesma (Figure 37).

Distribution and habitat: Guaymas, Sonora (27°55'N, 110°53'W) (CAS 066627), and La Paz, Baja California Sur (24°10'N, 110°19'W) (Skoglund Coll.), south to Tumbez, Tumbez Prov., Peru (3°40'S, 80°23'W) (PRI 25945), on intertidal mudflats. This species is known from only 6 lots, including the type specimen.

Bushia DALL, 1886:309–311

Type species: *Asthenothaerus* (*Bushia*) *elegans* Dall, 1886; by monotypy—western Atlantic [see also DALL, 1889:440; pl. 39, fig. 1].

This genus has a small segment of external ligament and a large internal one with a conspicuous, bar-shaped lithodesma seated on thickened cups beneath the beaks (Figure 41). In *Bushia* s.s., these cups are on the shell wall. In *B. (Pseudocyathodonta)*, they are on a shelf between the shell wall and the hinge plate.

Subgenus (*Bushia*) s.s.

The four known species of *Bushia* (*Bushia*) have concentric sculpture, prominent in three of them, subdued in the fourth. All occur offshore. DALL (1886) described the anatomy of *B. elegans*. The type species occurs in the western Atlantic, the other three in the eastern Pacific.

Bushia (*B.*) *panamensis* (Dall, 1890)

(Figure 38)

Asthenothaerus (*Bushia*) (*elegans* var.?) *panamensis* Dall, 1890: DALL, 1890:275; DALL, 1915:446 [*Bushia* as a full genus]; KEEN, 1958:231; fig. 592; KEEN, 1971:296–297; fig. 763; BERNARD, 1983:64.

Type material and locality: USNM 87583, holotype, a right valve; length, 13.9 mm; height, 11.2 mm; convexity, 3.6 mm (pair would have been about 7.2 mm) (Figure 38). SW of Isla San José, Archipiélago de las Perlas, Gulf of Panama (7°56′N, 79°41′30″W); 94 m; mud; USFC Sta. 2805; 30 Mar. 1888.

Description: Small (length, 13.9 mm), oval, inflated, approximately equilateral; anterior end sharply rounded; posterior end slightly truncate; surface with strong concentric sculpture; pallial line reaching just short of midline.

Distribution and habitat: Known only from the type specimen.

Discussion: In describing the type species of *Bushia* as well as this species, Dall regarded *Bushia* as being a subgenus of *Asthenothaerus*, but his headings cite the species as if *Bushia* were a full genus. Because his intent is clear, parentheses must be placed around Dall's name when *Bushia* is used as a full genus.

Of the three eastern Pacific and one western Atlantic species of *Bushia*, this one differs in being more inflated, proportionately higher for its length, and in having more central beaks.

Bushia (*B.*) *galapagana* (Dall, 1915)

(Figure 39)

Cyathodonta galapagana Dall, 1915
    DALL, 1915:446.

Type material and locality: USNM 195029, holotype, a left valve; length, 25.9 mm; height, 16.9 mm; convexity, 5.0 mm (Figure 39). Off Isla Gardner, Galápagos Islands, Ecuador (1°21′S; 89°40′15″W); 73 m; sand; USCF Sta. 2813; 7 Apr. 1888.

Description: Medium-sized (length to 32.8 mm; SBMNH 35093; Isla del Coco, Costa Rica), elongate; anterior end longer, sharply rounded; posterior end truncate; externally with conspicuous concentric sculpture (somewhat subdued on central ventral margin of holotype, but not in material from Isla del Coco); pallial sinus just reaching vertical line from beaks.

Distribution and habitat: Known from just four stations: three in Bahía Chatham, Isla del Coco, Costa Rica (5°33′N, 87°2′30″W) (LACM 38–39; SBMNH 35093, 35094), and the type specimen from the Galápagos Islands (1°21′S, 89°40′15″W) (USNM 195029); 57–83 m (mean, 71 m).

Discussion: This species has been overlooked by many workers and is not mentioned by KEEN (1958, 1971), OLSSON (1961), or BERNARD (1983).

Dall, who had described the genus *Bushia* and both of its then-known species, did not recognize that this species was another *Bushia*. Instead, he placed it in *Cyathodonta*, which has a very different ligament, with a resilifer on the hinge plate and no deeply seated lithodesma.

Of the eastern Pacific species of *Bushia*, this is closest to the type species, *B. elegans* from the western Atlantic, differing in being much larger and in having heavier, more widely spaced concentric ribs.

Bushia (*B.*) *phillipsi* Coan, sp. nov.

(Figures 40, 41)
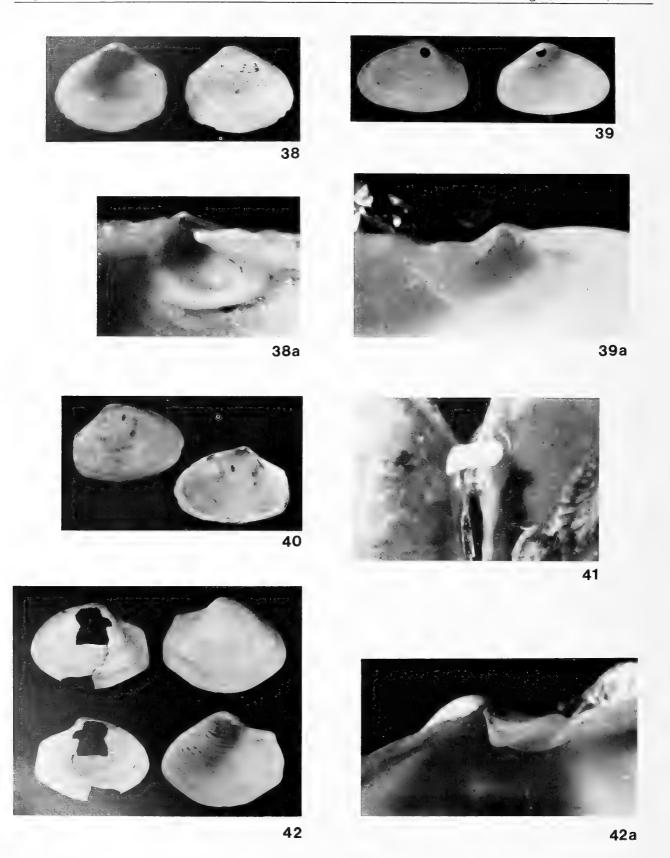
Type material and locality: SBMNH 35095, holotype, right valve; length, 23.0 mm; height, 16.4 mm; convexity, 4.5 mm (Figure 40). SBMNH 35096, paratypes, one smaller right valve and two still smaller pairs. The lithodesma of one of these pairs is illustrated here (Figure 41). N end Isla Smith, Gulf of California, Baja California Norte (29°6′N, 113°31′W); 183 m; C. & P. Skoglund; Nov. 1981.

Skoglund Coll., paratypes, 2 left valves. W end of Isla Smith, Baja California Norte (29°4′N, 113°31′W); 114–152 m; C. & P. Skoglund; Apr. 1988.

Description: Small (to 23 mm; holotype), thin-shelled; right valve more inflated; anterior end longer, sharply rounded; posterior end truncate; sculpture of very subdued concentric ribs; pallial sinus broad, short; lithodesma bar-shaped, seated in thickened cups on shell wall under umbones.

Differentiation: *Bushia* *phillipsi* differs from the other species in the subgenus in its subdued concentric ribs and its thin shell; each of the other species has a heavier shell and more conspicuous concentric sculpture. It is less elongate than *B. galapagana*, but more so than *B. panamensis*. It is larger than any specimens thus far obtained of either *B. panamensis* or *B. elegans*.

Distribution and habitat: Known only from four stations on the western side of the Gulf of California, from Isla

38

39

38a

39a

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41

42

42a

Smith (29°6'N, 113°31'W) (type lots), to off Isla Danzante (25°48'N, 111°16'W) (SBMNH 35097; Skoglund Coll.); 38–183 m (mean, 104 m); no bottom types recorded.

In addition to the type lots, this species is represented in collections by the following material:

SBMNH 35097—off Isla Danzante, 61 m—2 valves
Skoglund Coll.—off Isla Danzante, 31–46 m—4 valves.

Discussion: This species is named for David W. Phillips of Davis, California, editor-in-chief of *The Veliger*.

Bushia (*Pseudocyathodonta*) Coan, subgen. nov.

Type species: *B.* (*P.*) *draperi* Coan, sp. nov.—eastern Pacific.

The shells of this new subgenus are shaped like those of *Cyathodonta* and are of similar thickness, but they have a hinge similar to that in *Bushia*. There is a somewhat projecting resilifer for the external portion of the ligament, but it is much smaller than that in *Cyathodonta* and lacks a thickened calcareous pad. A subumbonal cup on a shelf, well below the hinge plate, undoubtedly holds a lithodesma, which is lacking in the only known specimen. In *Bushia* s.s. the cup is on the shell wall. There is heavy concentric sculpture, but it is not oblique, as in *Cyathodonta*); it is more undulating than that in *Bushia* s.s.

This genus is known only from the type species.

Bushia (*Pseudocyathodonta*) *draperi* Coan, sp. nov.

(Figure 42, 42a)

Type material and locality: SBMNH 35098, holotype, pair; length, 28.5 mm; height, 22.4 mm; convexity, 12.2 mm [broken] (Figure 42). In the Gulf of California, off Isla Danzante, Baja California Sur (25°48'N, 111°16'W); 61 m; C. & P. Skoglund; either Oct. 1979 or Oct. 1983.

Description: Small (to 28.5 mm in length; holotype), thin; right valve larger, more inflated; approximately equilateral; anterior end sharply rounded; posterior end set off by a low ridge, truncate; escutcheon present, most evident in left valve; surface with conspicuous concentric sculpture, which becomes finer toward posterior end; posterior end with fine pustules; hinge plate narrow, with a subumbonal

cup on a shelf beneath the beaks that presumably holds a lithodesma.

Distribution and habitat: Known only from the holotype.

Discussion: This species is named for Bertram C. Draper of Los Angeles, California, who has helped with the photographic work for many papers by various authors.

Lampeia MacGinitie, 1959

Type species: *Thracia* (*Lampeia*) *adamsi* MacGinitie, 1959, by original designation—Arctic coast of Alaska.

A narrow segment of external ligament is present along the dorsal margin, but the main ligament is internal, attached to an oblique structure on the shell wall under the beaks. This structure is free along its anteroventral margin, where it is supported by a series of pillars. The internal ligament is supported by a strong, curved lithodesma. The outside of the shell is covered by a heavy brown periostracum.

The hinge of this genus is closest to *Asthenothaerus*, but its shell is much heavier than that of this genus; it has a thick, dark periostracum; and there is a simple, curved lithodesma. The buttressed subumbonal structure is like nothing else. This genus is represented only by the following species.

Lampeia adamsi (MacGinitie, 1959)

(Figures 43, 44)

Thracia (*Lampeia*) *adamsi* MacGinitie, 1959:
MacGINITIE, 1959:163–164; pl. 18, fig. 9; pl. 21, figs. 7, 8; pl. 24, fig. 8.

Type material and locality: USNM 610301, holotype, pair; length, 22.8 mm; height, 18.3 mm; convexity, 9.7 mm (Figure 43). 4 km off Point Barrow, Arctic coast of Alaska (about 71°31'N, 156°23'W); 33.5 m, mud-gravel-stone bottom; G. E. MacGinitie, 15 Sept. 1948.

Description: Small (to 29.7 mm; UAM 4473; NW Bering Sea); shells average in thickness; right valve larger, more inflated; anterior end slightly longer, rounded; posterior end truncate, with an escutcheon that is evident in both valves; lunule present in left valve; surface of adults with

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←
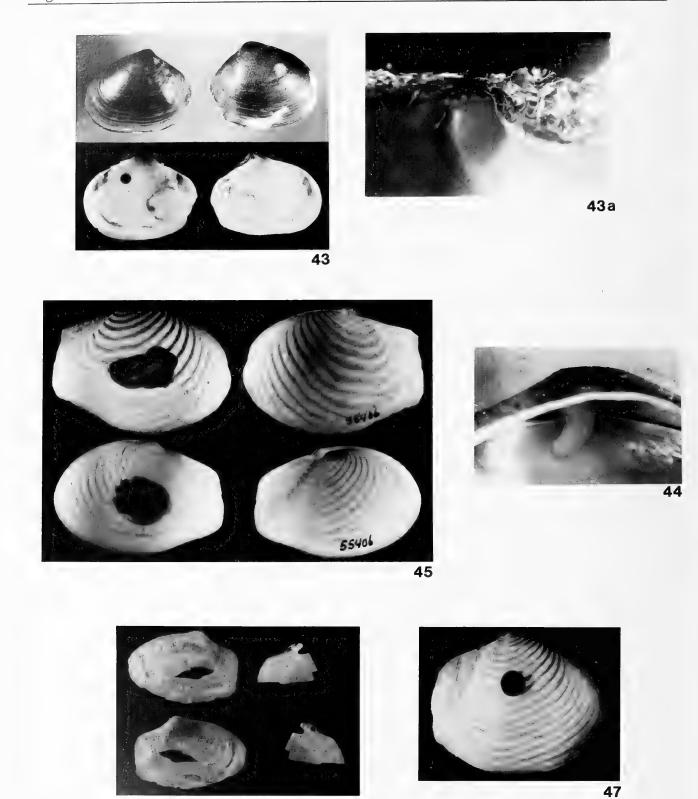
Explanation of Figures 38 to 42

Figure 38. *Bushia* (*B.*) *panamensis* (Dall). Holotype of *Asthenothaerus* (*B.*) *panamensis*; USNM 87583; length, 13.9 mm. Figure 38a: Close-up of subumbonal cup for lithodesma.

Figure 39. *Bushia* (*B.*) *galapagana* (Dall). Holotype of *Cyathodonta galapagana*; USNM 195029; length, 25.9 mm. Figure 39a: Close-up of subumbonal cup for lithodesma.

Figures 40, 41. *Bushia* (*B.*) *phillipsi* Coan, sp. nov. Figure 40: Holotype; SBMNH 35095; length, 23.0 mm. Figure 41: Paratype; SBMNH 35096; close-up showing lithodesma under beaks.

Figure 42. *Bushia* (*Pseudocyathodonta*) *draperi* Coan, subgen. et sp. nov. Holotype; SBMNH 35098; length, 28.5 mm. Figure 42a: Close-up of hinge of right valve showing resilifer and subumbonal cup for lithodesma.

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43a

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Explanation of Figures 43 to 47

Figures 43, 44. *Lampeia adamsi* (MacGinitie). Figure 43: Holotype of *Thracia* (*L.*) *adamsi*; USNM 610301; length,
22.8 mm. Figure 43a: Close-up of right valve showing subumbonal slot for lithodesma. Figure 44: CAS 066628;
off Point Barrow, Alaska; 39 m; length, 11.4 mm; close-up of a broken pair showing lithodesma.

heavy, dark periostracum and concentric growth lines; pallial sinus short, broad.

Distribution and habitat: On the Arctic coast of Alaska, from off Point Barrow (71°34'N, 156°22'W) (CAS 066628), westward into the NW Bering Sea off Mys Chaplino, Chukotskiy Poluostrov (64°18'30"N, 171°8'W) (UAM 4473); 10–41 m (mean, 28 m). Sediment type is recorded only for the type specimen: mud-gravel-stone bottom. I have examined 8 lots, including the type.

Cyathodonta CONRAD, 1849a:155–156

Type species: *C. undulata* Conrad, 1849a; by monotypy—eastern Pacific.

Shells with conspicuous, oblique, undulating sculpture; hinge with an external ligament and a projecting resilifer; resilifer thickened with a calcareous pad; a small, curved lithodesma present on anterior surface of resilium.

There are at least four other species in addition to four in the eastern Pacific:

C. cruziana DALL, 1915:446—western Atlantic
C. granulosa (A. ADAMS & REEVE, 1850:82, 87; pl. 23, fig. 16)—Japan
C. plicata (DESHAYES, 1832:1039–1040)—west Africa
C. rugosa (LAMARCK, 1818:464)—western Atlantic [synonyms: *Thracia magnifica* JONAS, 1850:170; pl. 4, fig. 7; *T. semirugosa* REEVE, 1859:pl. 2 (*nomen nudum*); *T. plicata* (Deshayes), *auctt., non* Deshayes, 1832; *T. (C.) dalli* MANSFIELD, 1929:7, 10; pl. 4, figs. 1, 2; *T. dissimilis* GUPPY, 1875:52; *C. rectangulata* MACSOTAY, 1968:87–88, 410; pl. 4, figs. 1, 2—see Discussion under *C. undulata*].

Cyathodonta undulata Conrad, 1849

(Figures 45–47)

Cyathodonta undulata Conrad, 1849:
    CONRAD, 1849a:155–156; CONRAD, 1849b:230; CARPENTER, 1864b:633 [1872:119]; CONRAD, 1869:53; DALL, 1915:444; GRANT & GALE, 1931:259 [in part; not figs.]; LAMY, 1931:285–286; HERTLEIN & STRONG, 1946:96; HERTLEIN & STRONG, 1955:181; pl. 3, figs. 1, 2; KEEN, 1958:232–233; fig. 595; OLSSON, 1961:459; KEEN, 1971:297, 299; fig. 766; BERNARD, 1983:64.
Cyathodonta granulosa (Adams & Reeve), *auctt., non* Adams & Reeve, 1850:
    GOULD, 1853:407 [species' author not given; *nomen nudum*]; CARPENTER, 1857b:231 [as "*C. granulosa* Gould"; *nomen nudum*]. [*non Thracia granulosa* A. ADAMS & REEVE, 1850:82, 87; pl. 23, fig. 16.]
Thracia plicata Deshayes, *auctt., non* Deshayes, 1832:
    CARPENTER, 1857b:231, 297, 352; REEVE, 1859:pl. 2, fig. 7b, c [not 7a] [according to LAMY, 1931:285]; CARPENTER, 1864b:541, 564, 619 [1872:27, 50, 105]; CONRAD, 1869:53; STEARNS, 1894:157; LAMY, 1909:253. [*non* DESHAYES, 1832:1039.]

Thracia magnifica Jonas, *auctt., non* Jonas, 1850:
    MABILLE, 1895:76. [*non* JONAS, 1850:170; pl. 4, fig. 7.]
Cyathodonta lucasana Dall, 1915:
    DALL, 1915:445; HERTLEIN & STRONG, 1946:96 [in part; not figs.]; KEEN, 1958:232 [in part; not figs.]; KEEN, 1971:297 [in part; not figs.]; BERNARD, 1983:64. [but not *C. lucasana* Dall, *auctt.,* =*C. dubiosa*—which see.]
Cyathodonta dubiosa Dall, *auctt., non* Dall, 1915:
    DURHAM, 1950:70, 161; pl. 16, figs. 2, 7. [*non* DALL, 1915:445.]
Cyathodonta undulata peruviana Olsson, 1961:
    OLSSON, 1961:459, 556; pl. 83, fig. 2–2b; KEEN, 1971:297 [as a synonym of *C. undulata*]; BERNARD, 1983:64 [as a synonym of *C. undulata*].

Type material and localities: *C. undulata*—ANSP 55406, **lectotype (herein),** pair; length, 48.5 mm; height, 35.0 mm; convexity, 15.3 mm (Figure 45). ANSP 372699, paralectotype, a smaller pair. "Coasts of Lower California and Peru"; restricted to the east coast of Baja California by HERTLEIN & STRONG (1946:96); **here further clarified as being La Paz, Baja California Sur** (24°12'N, 110°22'W), where the species has been taken (for example, LACM 60-7).

C. lucasana—USNM 15910b, holotype, left valve; length 7.8 mm; height, 5.3 mm; convexity, 1.3 mm (Figure 46). Cabo San Lucas, Baja California Sur (22°52'N, 109°54'W); J. Xantus.

C. undulata peruviana—ANSP 218953, holotype, right valve; length, 49.2 mm; height, 39.0 mm; convexity, 10.9 mm (Figure 47). Puerto Pizarro [Tumbez], Tumbez Prov., Peru (3°29'S, 80°23'W); A. A. Olsson, 1958.

Description: Medium-sized (length to 50.2 mm; SBMNH 35099; Puertecitos, Baja California Norte), oval; right valve much more inflated; anterior end longer, rounded; posterior end set off, truncate; surface with oblique concentric undulations, strongest on anterior end, and pustules that generally form a radial pattern (pattern most evident on central part of valves); posterior end more densely pustulose; periostracum tan, evident only on posterior slope; pallial sinus moderate in length, reaching almost to vertical line from beaks.

Distribution: Bahía Magdalena, Baja California Sur (24°38'N, 112°9'W) (LACM 140427), throughout the Gulf of California, south to Punta Organos, Peru (4°8'S, 81°7'W) (CAS 066629); Isla San Cristóbal, Galápagos Islands (LACM 38-188). Most lots are beach material; live-collected material has been obtained from the intertidal zone to 64 m (mean, 14 m). The bottom type most often recorded is sand. I have examined 109 lots, including the type material.

This species has been reported in Pliocene strata of the Imperial Formation in southern California (HANNA, 1926: 466; POWELL, 1988:16) and of Isla Carmen, Baja Cali-

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Figures 45–47. *Cyathodonta undulata* Conrad. Figure 45: **Lectotype (herein)**; ANSP 55406; length, 48.5 mm. Figure 46: Holotype of *C. lucasana* Dall; USNM 15910b; length, 7.8 mm. Figure 47: Holotype of *C. undulata peruviana* Olsson; ANSP 218953; length, 49.2 mm.

fornia Sur (EMERSON & HERTLEIN, 1964:342, 349). It has also been recorded in formations of Pleistocene age at Bahía Magdalena, Baja California Sur (JORDAN, 1936:112, 123), and on the Burica Peninsula, Panama (OLSSON, 1942:162). HOFFSTETTER (1952:45) reported it as a "subfossil" on the Santa Elena Peninsula, Ecuador. Records in Pleistocene formations in southern California need to be reexamined (see Discussion under *Cyathodonta pedroana*).

Discussion: There is a similar *Cyathodonta* in the western Atlantic, and I am unable to differentiate *C. undulata* from some specimens of this rare species. The earliest name for the Atlantic species appears to be *Anatina rugosa* LAMARCK, 1818 (p. 464), described from Santo Domingo [Hispaniola]. The holotype, a right valve measuring 41.7 mm in length, is in the Muséum d'Histoire Naturelle, Geneva (No. 1082/36) (Figure 48). I have seen only a few specimens of this species, and these not simultaneously, and it is possible that more than one taxon is involved. Large, intact specimens were discussed and figured by J. GIBSON-SMITH & W. GIBSON-SMITH (1983:181; figs. 11–13). Caribbean material attains a larger size (73 mm) than *C. undulata,* and these authors maintain that it is more produced anteriorly than is *C. undulata.* However, the shape of the anterior end is variable in *C. undulata,* and this may prove to be the case with the Caribbean species.

Cyathodonta lucasana is based on a broken, juvenile *Cyathodonta.* Although no other available material is this small, it seems to match *C. undulata* most closely. The name *C. lucasana* has been misapplied to specimens of *C. dubiosa* Dall.

Cyathodonta undulata peruviana falls within the range of variability of this species, and oval specimens matching its type have also been obtained in the Gulf of California.

Cyathodonta dubiosa Dall, 1915

(Figure 49)

Cyathodonta dubiosa Dall, 1915:
DALL, 1915:445; I. OLDROYD, 1925:86; pl. 9, fig. 5; HERTLEIN & STRONG, 1946:96; KEEN, 1958:232–233; fig. 593; KEEN, 1971:296–297; fig. 764; BERNARD, 1983: 64.
Cyathodonta lucasana Dall, auctt., non Dall, 1915:
HERTLEIN & STRONG, 1946:96, 120; pl. 1, figs. 4, 9; KEEN, 1958:232–233; fig. 594; KEEN, 1971:296–297; fig. 765. [non DALL, 1915:445.]
[non *C. dubiosa* Dall, auctt., =*C. undulata* or *C. pedroana*—see under these species.]

Type material and locality: *C. dubiosa*—USNM 96450, holotype, right valve; length, 38.1 mm; height, 27.8 mm; convexity, 8.0 mm (Figure 49). Off La Paz, Baja California Sur (24°18'N, 110°22'W); 48 m; sand; USCF Sta. 2823, 30 Apr. 1888.

Description: Medium-sized (length to 40.2 mm; Skoglund Coll.; off Tetas de Cabra, Sonora, Mexico), oval to elongate-oval; right valve somewhat more inflated; equilateral,

or longer either posteriorly or anteriorly, these variations present within a single lot; concentric undulations generally lower, more numerous and less oblique than those in *Cyathodonta undulata;* punctations denser than in the preceding species, generally arranged in concentric rows; periostracum tan; pallial sinus very shallow.

Distribution and habitat: In Mexico, from Isla Smith, Baja California Norte (29°3'N, 113°30'W) (SBMNH 35100; Skoglund Coll.), and Punta San Antonio, Sonora (27°57'N, 111°7'W) (SBMNH 35101), to Salina Cruz (16°9'N, 95°12'W) (Skoglund Coll.) and Puerto Huatulco (15°44'30"N, 96°8'W) (CAS 066630), Oaxaca; 13 to 183 m (mean, 96 m). The only bottom type recorded, this on but one lot, is sand. I have examined just 11 lots, including the type.

Records of this species from California (DALL, 1915; I. OLDROYD, 1925) are based on misidentifications of *Cyathodonta pedroana.*

This species has been recorded from Pleistocene strata at Bahía Magdalena, Baja California Sur (JORDAN, 1936: 112) and on the Burica Peninsula, Panama (OLSSON, 1942: 162).

Discussion: In northern Mexico, this species occurs with *Cyathodonta undulata,* from which it can be separated by its more inflated left valve; denser punctations, which are arrayed in a concentric pattern; its finer, less oblique concentric undulations; its shallow pallial sinus; and its offshore habitat.

This rare species seems more closely related to a number of fossil taxa than does *Cyathodonta undulata.* These include: *C. gatunensis* (TOULA, 1909:757–758; fig. 15), from Miocene formations in Central America, which appears to have heavier, less oblique ribs (WOODRING, 1982:722; pl. 121, fig. 7); *"Cyathodonta?" dolicha* WOODRING, 1982 (pp. 721–722; pl. 91, fig. 22; ?pl. 121, fig. 8), from the middle Miocene Gatun Formation of Panama; and *C. tristani* (OLSSON, 1922:383; pl. 20, fig. 3) from the middle Miocene of Costa Rica. These three taxa may represent the same species. Also related may be *C. guadalupensis* DALL, 1903 (p. 1527; pl. 53, fig. 6) and *C. spenceri* DALL, 1903 (pp. 1527–1528; pl. 53, fig. 8), from a Miocene formation on Guadeloupe (according to WOODRING (1982: 722), these two names probably refer to the same species); and *C. reedsi* MAURY, 1920 (pp. 25–26; pl. 5, fig. 2), from a Miocene formation in Puerto Rico.

In the Recent fauna, *Cyathodonta dubiosa* is closest to the western Atlantic *C. cruziana* Dall, 1915, which differs in being still more densely pustulose.

Cyathodonta pedroana Dall, 1915

(Figure 50)
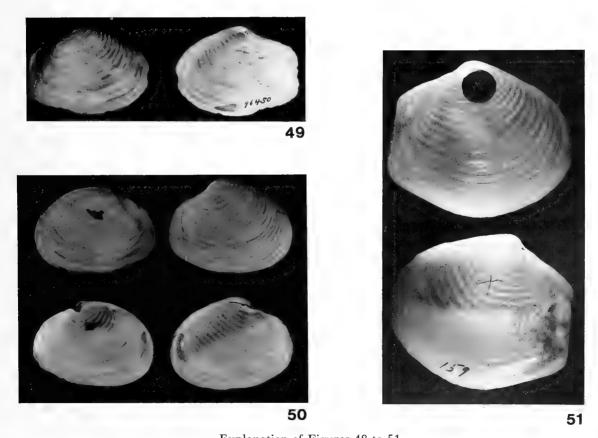
Cyathodonta pedroana Dall, 1915:
DALL, 1915:445; I. OLDROYD, 1925:86; pl. 54, figs. 1–3; BERNARD, 1983:64 [as a synonym of *C. dubiosa* Dall].
Cyathodonta dubiosa Dall, auctt., non Dall, 1915:
DALL, 1915:445 [in part; not type specimen].

48

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51

Explanation of Figures 48 to 51

Figure 48. *Cyathodonta rugosa* (Lamarck). Holotype of *Anatina rugosa*; MHNG 1082/36; length, 41.7 mm.

Figure 49. *Cyathodonta dubiosa* Dall. Holotype; USNM 96450; length, 38.1 mm.

Figure 50. *Cyathodonta pedroana* Dall. **Lectotype (herein)**; USNM 207527; length, 26.0 mm.

Figure 51. *Cyathodonta tumbeziana* Dall. Holotype; ANSP 218952; length, 37.6 mm.

Cyathodona undulata Conrad, *auctt., non* Conrad, 1849 GRANT
　& GALE, 1931:259, 906; pl. 13, fig. 6a, b [in part]. [*non*
　CONRAD, 1849a:155–156.]

Type material and locality: USNM 207527, **lectotype**
(herein), pair; length, 26.0 mm; height, 19.8 mm; convex-
ity, 10.8 mm (Figure 50). USNM 859377, paralectotypes,
5 pairs; SBMNH 34284, paralectotype, 1 pair. San Pedro
Harbor, Los Angeles Co., California (33°43′N, 118°15′W),
mud; Eschnaur.

Description: Medium-sized (length to 38 mm; LACM
16956; Newport Bay, Orange Co., California), thin; right
valve more inflated; left valve less flattened than that in
Cyathodonta undulata; anterior end longer, rounded; pos-
terior end truncate; concentric undulations, on average,
intermediate between those of *C. undulata* and *C. dubiosa*
(lower, more numerous, and less oblique than those of *C.
undulata*; more prominent and oblique than those in *C.
dubiosa*); pustules arrayed in a concentric pattern; peri-
ostracum dark brown; pallial sinus shallow, but deeper
than that in *C. dubiosa*.

Distribution and habitat: Monterey Bay, Monterey Co.,
California (36°37′N, 121°52′30″W) (LACM 60-22;
UCMP 2395), to Bahía Magdalena, Baja California Sur
(24°58′15″N, 115°53′W) (USNM 212572), from 9 to 114
m (mean, 36 m). A wide variety of bottom types are re-
corded, including shale, rocks, sand, and mud. I have ex-
amined 58 lots, including the type specimens.

Records of living *Cyathodonta undulata* and *C. dubiosa*
from southern California are undoubtedly based on this
species.

Material from Pliocene and Pleistocene strata in south-
ern California and northern Baja California must be reex-
amined in light of the differentiating characters discussed
here. Most of the following records may have been based
on this species, though it is possible that *Cyathodonta un-
dulata* also occurred here in the late Pleistocene:

　Pliocene—DURHAM & YERKES (1964:27), as *C.* cf. *C. un-
　　dulata.*
　Early Pleistocene—T. OLDROYD (1925:4), as *C. pedroana*; A.
　　CLARK (1931:opp. p. 30), as *C.* cf. *pedroana*; and DeLONG
　　(1941:opp. p. 244), as *Thracia undulata.*
　Late Pleistocene—WILLETT (1937:387), as *Thracia* (*C.*) *un-
　　dulata*; and KANAKOFF & EMERSON (1959:22), as *C.
　　undulata.*
　Undifferentiated Pleistocene—ORCUTT (1921:19), as *C. du-
　　biosa.*

Discussion: DALL (1915:446) described *Cyathodonta cru-
ziana* from "Santa Cruz Island" in the West Indies, in-
dicating that it is "analogous" to *C. pedroana*, but it seems
closer to *C. dubiosa* (see under same).

Cyathodonta tumbeziana Olsson, 1961

(Figure 51)

Cyathodonta tumbeziana Olsson, 1961:
　OLSSON, 1961:460, 556; pl. 83, fig. 1, 1a [on pl. expl.

as "*C. tumbezensis*"; **first revision herein**]; KEEN, 1971:
297 [as a possible synonym of *C. undulata*]; BERNARD,
1983:64 [as a synonym of *C. undulata*].

Type material and locality: ANSP 218952, holotype,
right valve; length, 37.6 mm; height, 32.2 mm; convexity,
7.9 mm (pair would have been about 14 mm) (Figure 51).
Tumbez, Tumbez Prov., Peru (3°29′S, 80°23′W); A. A.
Olsson, 1958.

Description: Medium-sized (length to 37.6 mm; holo-
type), oval; right valve decidedly more inflated; approxi-
mately equilateral; anterior end rounded; posterior end
truncate, with a very narrow posterior slope; ventral mar-
gin produced posteroventrally; concentric undulations ob-
scure, overlain by fine beaded threads; posterior slope with
conspicuous pustules, less dense than in other species; peri-
ostracum dark tan; pallial sinus shallow.

Distribution and habitat: Golfo de Tehuantepec off Puer-
to Madero, Chiapas, Mexico (14°42′–52′N, 92°32′–42′W)
(SBMNH 35102), to Mancora, Tumbez Prov., Peru (4°6′S,
81°4′W) (OLSSON, 1961; specimen not examined, but as-
sumed to be correctly identified), 13–26 m (mean, 19 m).
This species is known from only 7 lots, of which I have
examined 5, including the type specimen.

Discussion: This is the most distinctive eastern Pacific
species of *Cyathodonta,* and it can be distinguished by its
oval outline, produced posteroventral margin, and its nar-
row posterior slope.

EXCLUDED TAXA

(1) *Tyleria fragilis* H. ADAMS & A. ADAMS, 1856 (p. 368;
pl. 97, fig. 3, 3a; new genus and species), was tentatively
placed in the Thraciidae by KEEN (1958:232–233; fig.
596). Later, it was discovered that the type specimen was
actually a *Sphenia* (KEEN, 1971:263; see also BERNARD,
1983:58).

(2) *Thracia carnea* Mörch, 1860 (p. 180), proved to be a
Tellina (KEEN, 1966b:13, 14; fig. 14a, b).

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Laubierinidae and Pisanianurinae (Ranellidae), Two New Deep-Sea Taxa of the Tonnoidea (Gastropoda: Prosobranchia)

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Abstract. The classification of the Tonnoidea is discussed based on new information about deep-sea species. Representative radulae, opercula, and larval shells are described and figured. The conclusions agree mainly with earlier classification, with the following exceptions: Oocorythinae is moved from Tonnidae to Cassidae and its value as a subfamily is questioned. The gross anatomies of two Recent deep-water species of *Pisanianura* Rovereto, 1899, are described, and a new ranellid subfamily, **Pisanianurinae**, is described for *Pisanianura* Rovereto, 1899, formerly classified in the Buccinidae. The genera *Laminilabrum* Kuroda & Habe, 1961, presently in the Trichotropidae, *Kaiparanura* Laws, 1944, and *Nawenia* Ladd, 1977, presently in the Buccinidae, are considered synonyms of *Pisanianura,* which is known in the fossil record since the Oligocene.

A new family, **Laubierinidae**, is erected for ***Laubierina*** gen. nov. and *Akibumia* Kuroda & Habe, 1958 (formerly Trichotropidae) with three Recent deep-water species. ***Laubierina peregrinator*** gen. et sp. nov. is described from deep water in the tropical Atlantic and Indian oceans. Two large (5 mm) planktonic larvae belonging to the **Laubierinidae** are described and one of them is remarkable for being a sexually mature male at the time of settlement. All dissected adults are females and it is speculated that ***Laubierina*** is a protandrous hermaphrodite with neotenic males. The gross anatomies of *L. peregrinator* sp. nov., *A. orientalis* (Schepman, 1909), and *A. schepmani* (Habe, 1962) are described.

Akibumia reticulata Habe, 1962, is referred to the Epitoniidae and *Conradia minuta* Golikov & Starobogatov, 1986 (described in Fossaridae) is considered a larva of Neptunellinae.

Thalassocyon bonus Barnard, 1960, and *T. tui* Dell, 1967, are synonymized; their anatomies are briefly described and compared with that of *Ficus* and it is concluded that *Thalassocyon* has been correctly referred to the Ficidae. Attention is drawn to the fact that the morphology of the Ficidae conforms poorly with other Tonnoidea.

The value and use of larval shells as taxonomical criteria are discussed, and it is concluded that they are useful criteria, as long as clear distinction is made between "primary" (*i.e.,* planktotrophic) and "secondary" (*i.e.,* non-planktotrophic) types of larval shells and only "primary" ones are compared.

INTRODUCTION

During the last two decades, several French expeditions have been exploring the bathyal and abyssal parts of the Indo-Pacific area. During these expeditions, material of deep-water species of the Tonnoidea has been obtained. Such specimens are rare and each expedition has usually brought back only one or two samples. Among them were

some specimens that could not be classified in the normally accepted suprageneric taxa.

During the same time, much has been added to the knowledge of the tonnoids, mainly through the work of Dr. Alan Beu, Geological Survey of New Zealand (see Literature Cited), working on the recent and fossil tonnoids. In order to give a more complete picture of the superfamily, we have felt that it would be valuable to review also the deep-sea groups, which otherwise, through their deviate morphology, might easily be overlooked.

We have also studied the consequences that the new taxa may have on existing classification by comparing them with presently accepted groups, and we have supplemented existing information with new data about larval shell and radular morphology of the known groups.

We will start by giving a key to the families of Tonnoidea partly based on BEU's (1981, 1988b) characters of the families, supplemented by our own observations. Then we continue with a review of the families of the Tonnoidea, supplemented by new information and illustrations of features used in the discussions of the new taxa. We finish with a discussion about the larval shell of the Tonnoidea and its value as a taxonomic criterion.

Author names and dates not found in the text are given in the Appendix.

MATERIAL

Deep-water Tonnoidea are rare and the material studied here has been accumulated over a period of more than 20 years. The following expeditions contributed material that was essential to our understanding of the deep-water Tonnoidea. "Benthedi," 1977, on R/V *Suroit,* in the northern part of the Mozambique Channel, directed by B. Thomassin, collected the first lot of **Laubierinidae**, which puzzled us for several years. "Walvis," 1981, on R/V *Jean Charcot,* off southwestern Africa, directed by M. Sibuet, collected additional wet material of **Laubierinidae**. "Biocal," 1985, on R/V *Jean Charcot,* off southern New Caledonia, directed by C. Levi, brought back living representatives of the genus *Pisanianura.* Other expeditions yielded additional information and are cited when appropriate in the text.

In addition, described and undescribed material from AMS, ANSP, MOM, NMNZ, SAM, SMNH, USNM, ZMA, and ZMC was examined. When necessary, type material has been examined, and is referred to in the text or accompanying figures.

The author and date for the taxa discussed are given at appropriate places in the text, except for the species listed in the Appendix.

ABBREVIATIONS USED

AMS, Australian Museum, Sydney; ANSP, Academy of Natural Sciences, Philadelphia; MNHN, Museum National d'Histoire Naturelle, Paris; MOM, Musée Océan-ographique, Monaco; NMNZ, National Museum of New Zealand, Wellington; NZGS, New Zealand Geological Survey, Lower Hutt; NZOI, New Zealand Oceanographic Institute; SAM, South African Museum, Cape Town; SMNH, Naturhistoriska Riksmuseet, Stockholm; USNM, U.S. National Museum of Natural History, Washington, D.C.; ZMA, Zoölogisch Museum, Amsterdam; ZMC, Zoologisk Museum, København.

SYSTEMATICS

Superfamily TONNOIDEA Suter, 1913

The superfamily Tonnoidea has been defined by THIELE (1929) and BOSS (1982). The only change in the criteria of this taxon that our investigations have necessitated is that the osphradium, which has been supposed to be bipectinate in all species, is monopectinate in the **Laubierinidae.** If future work shows that the Ficidae does not belong to the Tonnoidea (*cf.* p. 83), it should also be added that all Tonnoidea have large, complex salivary glands (small and simple in Ficidae).

Morphology of the Tonnoid Veliger

Veliger larvae belonging to species of Tonnoidea have been known since the mid-19th century oceanographic expeditions (FORBES, 1852; H. & A. ADAMS, 1853–1858), and these large larvae were then frequently described as distinct holoplanktonic species. The following generic names were thus based on tonnoid larvae: *Macgillivraya* Forbes, 1852, larva of *Tonna* Brünnich, 1772; *Calcarella* Souleyet, 1850, probably larva of *Distorsio* Röding, 1798; *Gemella* H. & A. Adams, 1858, a cassid; *Talisman* de Folin, 1884, a bursid larva; and *Dissentoma* Pilsbry, 1945 (see PILSBRY, 1949) and *Ethella* H. & A. Adams, 1858, neptunelline larvae. Empty larval shells in sediments were (and still occasionally are) given specific names before being recognized as larval shells.

CAZENAVETTE (1853) briefly and FISCHER (1863) in more detail described the young of *Tonna* and identified it with *Macgillivraya.* Several authors (*e.g.,* KESTEVEN, 1901, 1902; CLENCH & TURNER, 1957) then figured the larval shells of tonnoids, based on young benthic stages with preserved apical whorls. PELSENEER (1906) briefly described two ranellid larvae from the Bay of Biscay (as *Coralliophila* sp. A and B). SIMROTH (1911) described *Calcarella* in some detail, but did not see the connection with the adult stage. Finally, SCHELTEMA (1971, 1972) and LAURSEN (1981) on a larger scale identified and figured planktonic larvae by comparison with benthic stages. SCHELTEMA (1966) introduced the term "teleplanic" to characterize the long-lived veligers of Neptunellinae and demonstrated that trans-Atlantic dispersal could take place during their planktonic life. PECHENIK *et al.* (1984) have shown that planktonic larvae of *Cymatium parthenopeum* (von Salis, 1793) do not grow during their dispersal across the North Atlantic via the North Atlantic drift, but remain

competent for metamorphosis during periods extending over 300 days. This growth stasis and ability to delay metamorphosis explains the more or less circumtropical distribution for many species of Tonnoidea. (It does not explain, however, why many of them are absent in the tropical eastern Pacific, and most species despite having teleplanic larvae are not cosmopolitan.)

We have examined numerous species of Tonnoidea in order to find out to what extent and with what precision larval shells can be identified, because these frequently are encountered in samples of plankton and benthos, and also in order to find out if the larval shells give any clues about the systematic relations of the species. We have then supplemented comparison of larval shells from planktonic or benthic catches and young specimens with examination of opercula and radulae, which contain important information. Under each family we figure representative species, with operculum and radula.

A sculpture of thin axial and spiral cords that meet at right angles and are clearly set off from the smooth surface is present on protoconch II of at least some species in most families of Tonnoidea (Figures 79, 90, 92–96, 102–109, 110–113). This type of larval shell is here considered to indicate planktotrophic development. We are not convinced that certain other larval shells with reticulate sculpture built up by axial and spiral ribs, but lacking the smooth surface (*e.g.*, BEU, 1988b:fig. 1B), indicate planktotrophic development.

Key to the Recent Families and Subfamilies of Tonnoidea

A. Osphradium monopectinate, shell about as broad as high and without well-defined siphonal canal
.... **Laubierinidae**
A. Osphradium bipectinate, distinct siphonal canal present .... B
B. Operculum absent or reduced in adult C
B. Operculum well developed .... D
C. Siphonal notch present, larval shell corneous; if calcified, disjunctly coiled .... Tonnidae
C. Siphonal canal formed by the drawn out aperture; larval shell calcified, not disjunctly coiled .. Ficidae
D. Aperture with a well-developed posterior siphonal canal, jaws reduced; incremental scars aligned along both sides of shell, separated by 180° ..
.... Bursidae

D. Aperture without distinct posterior canal, jaws large
.... E
E. Shell globular or triangular with short siphonal canal .... Cassidae
E. Shell fusiform or bucciniform, often with long canal .... F
F. Parietal shield strongly developed; proboscis very long, strongly coiled when retracted; posterior edge of central radular tooth evenly curved ..
.... Personidae
F. Parietal shield not strongly developed; proboscis straight when retracted; posterior edge of central radular tooth straight ....G (Ranellidae)
G. Shell with regularly appearing varices .... H
G. Shell without varices .... **Pisanianurinae**
H. Varices separated about 240° ....Neptunellinae
H. Varices separated about 180° ....Ranellinae

Family RANELLIDAE Gray, 1854

(Figures 25–40, 52–55, 67–70, 85–95, 97–104, 123–127, 142–145, 153, 154)

BEU (1985) and BEU & CERNOHORSKY (1986) have pointed out the nomenclatorial reasons for using the name Ranellidae instead of the well-established and almost universally used name Cymatiidae, and Personinae instead of Distorsioninae. However, they have continued using Cymatiinae Iredale, 1913, as the name of the subfamily, referring to ICZN Article 40b. Because the Commission evidently refuses to consider invalidating the name Ranellidae, we can see no possibility to avoid using the name Neptunellinae introduced by GRAY (1854) at the same occasion as the Ranellidae. It is based on the generic name *Neptunella* Gray, 1854 (defined by citation of the name "[*Murex*] *cutaceum*" (Linné, 1758)) and is an objective junior synonym of *Cabestana* Röding, 1798. This is a regrettable consequence of the strict application of the Code.

BEU (1988b) convincingly separated the Personidae as a distinct family, present already in the Upper Cretaceous, and distinguished two subfamilies of Ranellidae:

Neptunellinae (=Cymatiinae), with a central radular tooth that is distinctly wider than high and is equipped with several lateral denticles; a periostracum with dense axial blades and varices separated by ⅔ of a whorl.
Ranellinae, with a central radular tooth equipped with a few lateral denticles and about as high as broad; a peri-
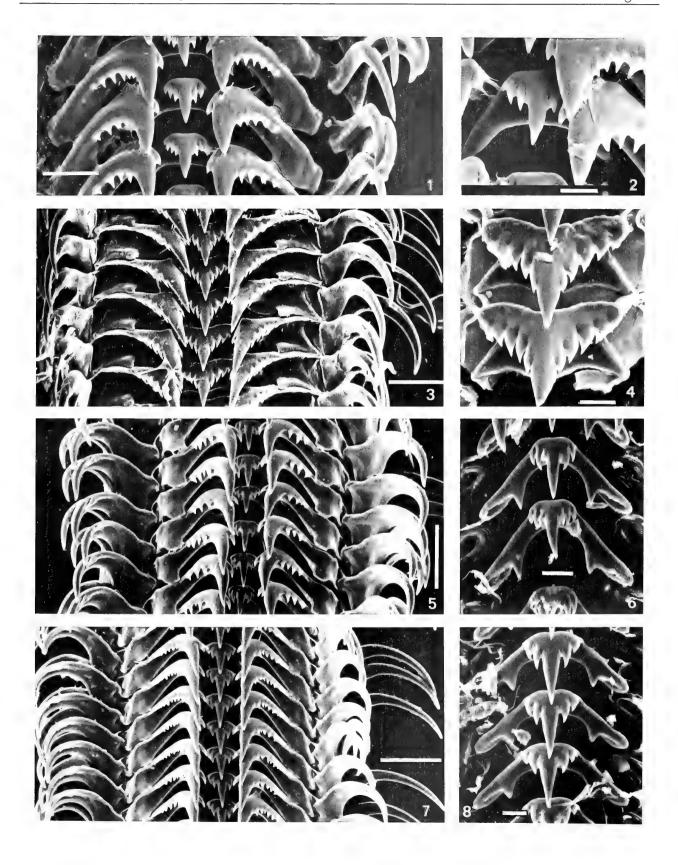
→

Explanation of Figures 1 to 8

Radulae of Ficidae and Bursidae.
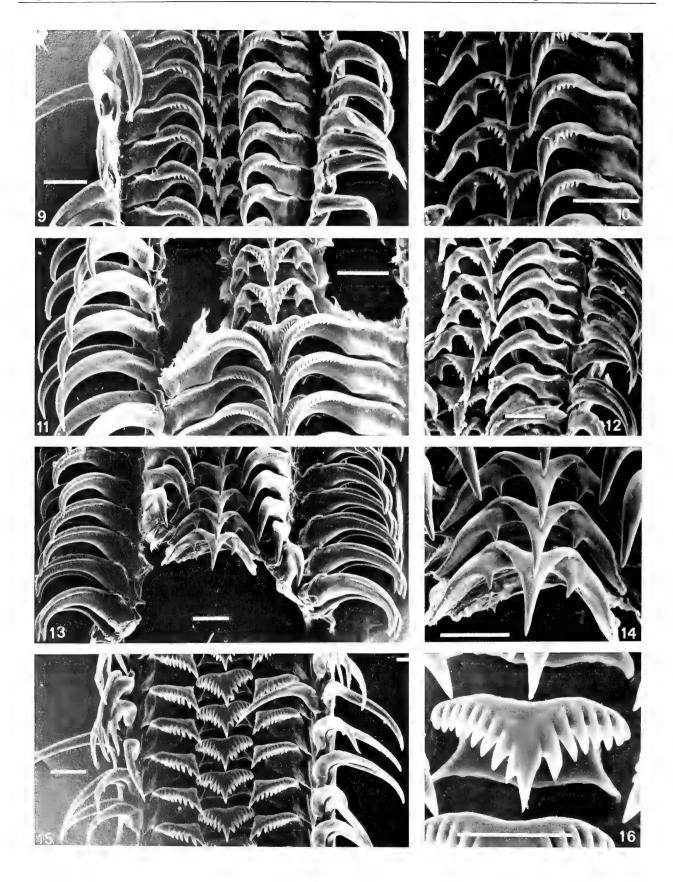
Figures 1 and 2. *Thalassocyon bonus* (New Zealand, NMNZ). Scale lines 25 and 10 μm.

Figures 3 and 4. *Ficus* sp. (Seychelles, MNHN). Scale lines 100 and 25 μm.

Figures 5 and 6. *Bursa* sp. (Gilbert Id., SMNH). Scale lines 100 and 25 μm.

Figures 7 and 8. *Bufonaria marginata* (Canaries, SMNH). Scale lines 100 and 25 μm.

ostracum without dense axial blades and varices aligned up the sides of the spire, *i.e.*, separated by 180°.

We will here add one additional subfamily, based on the genus *Pisanianura* Rovereto, 1899, previously classified in the Buccinidae. However, first we will give some background information about the protoconch of the Ranellidae.

The Ranellid Larval Shell

There is considerable variation in the morphology and development of the larval shell of this family. It is therefore outlined for the different subfamilies, and for species with planktotrophic development.

PILKINGTON (1974) described the early young of *Sassia* (*Cymatona*) *kampyla* (Watson, 1885) (Neptunellinae), which belongs to the oldest genus of Tonnoidea, dating back to the Late Cretaceous (Turonian, BEU 1988b). The planktonic stage of this species was mentioned by DELL (1956). In several papers Beu has later figured and described larval shells of many species of *Sassia*, which differ from other species of Neptunellinae in being calcareous, globular and often equipped with cancellate sculpture.

The morphology and biology of larvae belonging to *Cymatium* and *Charonia* (Neptunellinae) have been described by SCHELTEMA (1971), LAURSEN (1981), RICHTER (1984), and PECHENIK *et al.* (1984). Characteristic for these is that they are only partly, or not at all, calcified, and have a fairly tall spire, usually considerably higher than the aperture (Figures 97–104). The larval operculum has a characteristic shape, very slender, with a semicircular external and depressed bell-shaped inner margin (Figure 70). As in the Tonnidae the larval shell is, after settlement, filled by calcareous deposits, so that after destruction of the periostracum only a disjunctly coiled, internal mould remains. This internal mould shows the original sculpture also in species that resorb primarily deposited calcium carbonate (Figures 103, 104).

In species of *Sassia* (Neptunellinae)—*e.g., S. remensa* (Iredale, 1936), *S. parkinsonia* (Perry, 1811), and *Sassia raulini* (Cossmann & Peyrot, 1923) (Figure 90)—there is no interspace between the whorls of the protoconch II, even after treatment with bleach to remove remains of the periostracum. This can only be interpreted in one way, *viz.* that already the planktonic larva forms a calcareous shell, covered only externally by a periostracum.

We consider the sculpture of species of *Cymatium*, on the inside of the periostracum of the apical whorl (Figure 104) and on the remaining internal mould (Figure 103), of great interest and indicating that these species originate from species with a reticulate larval sculpture of the same type as in, *e.g., Sassia*.

The osphradium of the larva is usually bipectinate in species of *Cymatium*, but in one species we found a monopectinate osphradium (shell: see Figure 98).

The larvae of the Ranellinae are less well known, but PILKINGTON (1974, 1976) described the hatching young of *Argobuccinum pustulosum* (Lightfoot, 1786), *Fusitriton magellanicus*, and KESTEVEN (1901, 1902), IREDALE (1936), and BEU (1978a, b, 1988b) figured several protoconchs from juvenile specimens. To expand on this, we have examined some late larvae and early post-larvae. A specimen of *Ranella australasia* taken in surface plankton off southeastern Australia has a larval shell that shows only traces of an internal calcareous coating, which certainly is of no supporting function (Figure 89). The shell is perfectly smooth and unexpectedly solid, considering that it consists only of periostracum. Immediately after settlement the young starts to form an internal calcareous coating, and later a shell. When the post-larval growth continues, the periostracum starts to disintegrate and finally a perfectly smooth, calcareous, internal mould of the larval shell remains (as in Figures 86, 87), following the same pattern as in *Cymatium* and *Charonia*. We have examined young benthic stages of *Fusitriton magellanicus* (Figure 85), *Ranella olearia* (Figure 87), and *Argobuccinum pustulosum tumidum* (Figure 86) that have larval shells conforming with this developmental model. Usually one can see a distinct interspace between the whorls, where once there was periostracum (Figure 87).

The larval shell of the **Pisanianurinae** is characteristic in its large size (2.5–3.5 mm high), usually brown color, and globular shape without a distinct siphonal canal and especially in the perfectly reticulated sculpture with large smooth squares between raised axial and spiral ribs that meet at close to right angles (Figures 90, 96). It resembles that of the **Laubierinidae** (Figures 105, 106), but they have a still larger and proportionally broader larval shell (5–6 mm high) with an expanded aperture and a more regular spiral arrangement of the minute tubercles on protoconch I (*cf.* Figures 108 and 142).

Most competent ranellid larvae have a radula similar

Explanation of Figures 9 to 16
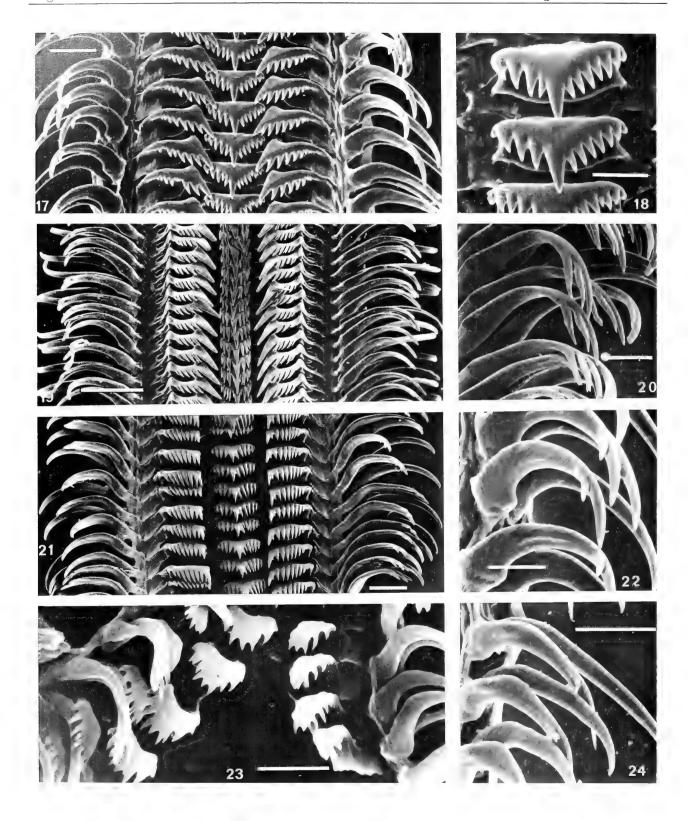
Radulae of Tonnidae and Cassidae.

Figures 9 and 10. *Tonna*, larva (off SE South Africa, SMNH). Scale lines 50 μm.

Figure 11. *Eudolium crosseanum* (the Azores, MNHN). Scale line 50 μm.

Figure 12. *Tonna* sp. (Madagascar, SMNH). Scale line 50 μm.

Figures 13 and 14. *Tonna allium* (Sumatra, SMNH). Scale lines 250 μm.

Figures 15 and 16. *Oocorys sulcata* (off S Portugal, MNHN). (For detail of marginal teeth, see Figure 24.) Scale lines 50 μm.

to adults of the species (Figures 30, 34, 36–38, 41, 42), but PELSENEER (1906:pl. 10, figs. 1–4) reported a species missing the radula and we noticed the same in a larva with a similar shell.

Subfamily PISANIANURINAE Warén & Bouchet, subfam. nov.

Diagnosis: Tonnoidea with a medium-sized *Buccinum*-like shell lacking varices, with poorly developed siphonal canal. Columella curved, contributing to giving the aperture a more rounded appearance. Operculum with corroded apical nucleus. Proboscis very short, broad, and muscular. Osphradium bipectinate with left row of leaflets less developed than inner ones.

Pisanianura Rovereto, 1899, has always been regarded as a buccinid genus, although FISCHER (1883) and LOCARD (1897) evidently had some doubts about it and compared *P. grimaldii* with *Oocorys*. We have had access to a few specimens preserved with soft parts and the anatomy (presented below) does not conform with a position in the Neogastropoda. The salivary glands have the typical structure that occurs only in Tonnoidea, and there is no deviation in other anatomical features from what is known in that superfamily. Therefore, we conclude that *Pisanianura* should be transferred to the Tonnoidea.

The shell morphology agrees well with the Ranellidae, except that it lacks varices (*i.e.,* it does not have periodical growth) and that the columella has a peculiar, curved shape. The anatomy is less useful for assigning *Pisanianura* to family because anatomical features, as far as they are known, are quite uniform throughout the superfamily and the differences so subtle and incompletely known that a detailed analysis can hardly be undertaken presently.

It is, however, obvious that the families are based on anatomical or shell morphological specializations, and because we are not suggesting anything better, we do not want to disturb this order. Therefore, we can exclude a position in the following families:

1. Ficidae. Salivary glands simple; proboscis pleurembolic, long and slender; buccal mass small and without large retractors.

2. Tonnidae. Foot large, operculum missing in adult; distal part of proboscis suckerlike; jaw with a strong hook; shell globular and inflated.

3. Bursidae. Jaws reduced or absent. Varices present. Posterior canal strongly developed.

4. Personidae. Proboscis very long and slender, coiled when retracted. Varices present.

5. Cassidae. Central radular tooth broad and low. Shell globular with short canal.

6. **Laubierinidae**. Osphradium monopectinate. Shell with poorly developed siphonal canal.

The Ranellidae on the other hand consists of species with obviously less specialized or modified morphology and we can see no reason against a position therein. (This may give reason to suspect that the classification is based on grades rather than clades, with the Ranellidae to some extent constituting a less modified stock. This may be true, but this classification is practical and in the absence of detailed anatomical information that gives a better resolution, we prefer to keep it.)

The assignment of *Pisanianura* to subfamily offers more problems. In the Neptunellinae the proboscis is retracted by numerous small muscles attached to the sheath (HOUBRICK & FRETTER, 1969), whereas in *Pisanianura* there are two major muscles attached to the buccal mass and additional muscles are inconspicuous. Another difference from the Neptunellinae is the relative size of the buccal mass, which in the Neptunellinae is small in relation to the proboscis sheath, whereas in *Pisanianura* it is large (for drawings of this see, *e.g.*: PANCERI, 1869; HALLER, 1893; SIMROTH, 1896–1907; AMADRUT, 1898; HOUBRICK & FRETTER, 1969).

It is difficult to compare anatomically *Pisanianura* with the Ranellinae because few species of that group have been described anatomically (HALLER, 1893), but it seems that the species of Ranellinae closely resemble the Neptunellinae. Also the shell morphology contradicts a position in the Ranellinae. Beu (pers. comm.) considers this a uniform, monophyletic taxon, characterized by the neat alignment of the varices along the sides, separated by 180°.

We, therefore, supported by Beu (pers. comm.), consider *Pisanianura* a monophyletic group distinct from the Neptunellinae and Ranellinae, and erect a new subfamily for *Pisanianura*, the **Pisanianurinae**, in the Ranellidae.

←

Explanation of Figures 17 to 24

Radulae of Cassidae.

Figures 17, 18, and 22. *Galeodea echinophora* (Mediterranean, SMNH). Scale lines 100, 50, and 50 μm.

Figures 19 and 20. *Semicassis granulatum* (Mediterranean, SMNH). Scale lines 500 and 100 μm.

Figure 21. *Semicassis saburon* (West Africa, MNHN). Scale line 100 μm.

Figure 23. *Cypraecassis testiculus,* larva from plankton (Dana sta. 1286). Scale line 10 μm.

Figure 24. *Oocorys sulcata,* marginal teeth (off S Portugal, MNHN). (For a figure of the whole radula, see Figure 15.) Scale line 100 μm.

It is also possible that the **Pisanianurinae** should be considered a distinct family in the Tonnoidea, because it (1) lacks varices, which evidently is a primitive character in the group and (2) has the left row of leaflets in the osphradium less developed (equal size in all other tonnoids except the **Laubierinidae**). This view is supported by Beu (pers. comm.).

The subfamily Anochetinae Cossmann, 1901, was erected with *Pisanianura* as "type genus" (in the Buccinidae), but it is not based on a generic name and therefore has no nomenclatural status.

Pisanianura Rovereto, 1899

Anura BELLARDI, 1873:201 (not *Anura* Hodgson, 1841). Type species: *Murex inflatus* Brocchi, 1814, subsequent designation COSSMANN (1901:178).

Pisanianura ROVERETO, 1899:104, new name for *Anura* Bellardi, 1873 (preoccupied several times).

New synonyms:

Kaiparanura LAWS, 1944:309. Type species by original designation: *Phos spiralis* Marshall, 1918, Miocene, New Zealand (Figures 142–145).

Laminilabrum Kuroda & Habe *in* HABE, 1961, app.:13. Type species by original designation: *L. breviaxe* Kuroda & Habe, 1961, Recent, deep water, Japan.

Nawenia LADD, 1977:51. Type species by original designation: *N. bartholomewi* Ladd, 1977, Pliocene, west Pacific.

Remarks: *Laminilabrum* was described in the Trichotropidae, *Kaiparanura* in the Cominellidae (=Buccinidae), and *Nawenia* in the Buccinidae. These positions have not been questioned since. The soft parts of *Pisanianura* and *Laminilabrum* (described after the species, below) do not indicate differences other than of specific rank. The shells of all four genera have in common a multispiral protoconch with a large-meshed reticulate sculpture, a teleoconch without varices, and a stongly curved columella. They differ mainly in the degree of axial sculpture on the teleoconch, with *Laminilabrum* having no axial sculpture, *Nawenia* axial sculpture on the first two whorls, and *Pisanianura* and *Kaiparanura* on all the whorls. We regard these differences as of specific rank, and consequently treat the generic names as synonyms.

The type species of *Pisanianura* is a Pliocene fossil from northern Italy. Brocchi's type material has been figured by ROSSI RONCHETTI (1955:201) and PINNA & SPEZIA (1978:pl. 34, fig. 3) and we have examined Pliocene material from Pradalbino, Bologna, Italy, kindly sent on loan by Mr. Della Bella (Figures 93, 125). The larval shell is multispiral with cancellate sculpture (Figure 93) and the teleoconch differs from the recent *P. grimaldii* mainly in the presence of a peripheral keel.

Beside the type species, BELLARDI (1873) included *Fusus borsoni* (Gené *in* Bellardi & Michelotti, 1840) in *Anura* and described *A. ovata, A. striata, A. craverii, A. pusilla,* and *A. sublaevis* from the Italian Miocene and Pliocene. We have not examined these species, some of which recently have been figured by FERRERO MORTARA *et al.* (1981:pl. 7). Judging from the figures it seems certain that the Miocene *A. craverii* belongs to *Pisanianura*; the status of the other species is more doubtful.

The genus is furthermore represented in the European Tertiary deposits by *Pisanianura aturensis* Peyrot, 1927, and *P. benoisti* Peyrot, 1927, from the Oligocene and Miocene of southwestern France respectively. (*P. degrangei* Peyrot, 1927, is probably a young cerithid related to *Gourmya* Fischer, 1884 [Cerithidae]; P. Lozouet, pers. comm.)

The type species of *Kaiparanura* is a Lower Miocene fossil from New Zealand; the teleoconch has a sculpture of coarse axial ribs. LAWS (1944) introduced this new genus because he had been misled by COSSMANN's (1901) description of the protoconch of *Pisanianura inflata*, which erroneously had been described as sculptured with weak spiral threads and with a smooth and depressed nucleus. This synonym was pointed out to us by Dr. A. Beu.

Finally, the type species of *Nawenia* is a Pliocene fossil from Fiji, similar to *Pisanianura breviaxe* but differing in having stronger axial sculpture on the first two teleoconch whorls.

Pisanianura is thus known from at least two Paleogene and two Neogene North Atlantic species, two Neogene South Pacific species, and two Recent (sub)tropical deepwater species. The taxonomy and distribution of the Recent species only are here treated in detail.

Pisanianura grimaldii (Dautzenberg, 1889)

(Figures 25, 26, 55, 68, 94, 95, 126, 127)

Hindsia grimaldii DAUTZENBERG, 1889:33, pl. 2, fig. 4.
Anura clathrata DAUTZENBERG & FISCHER, 1906:25, pl. 3, figs. 6–8. (New synonym.)

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Explanation of Figures 25 to 32

Radulae of Ranellidae.

Figures 25 and 26. *Pisanianura grimaldii* (New Caledonia, MNHN). Scale lines 50 μm.
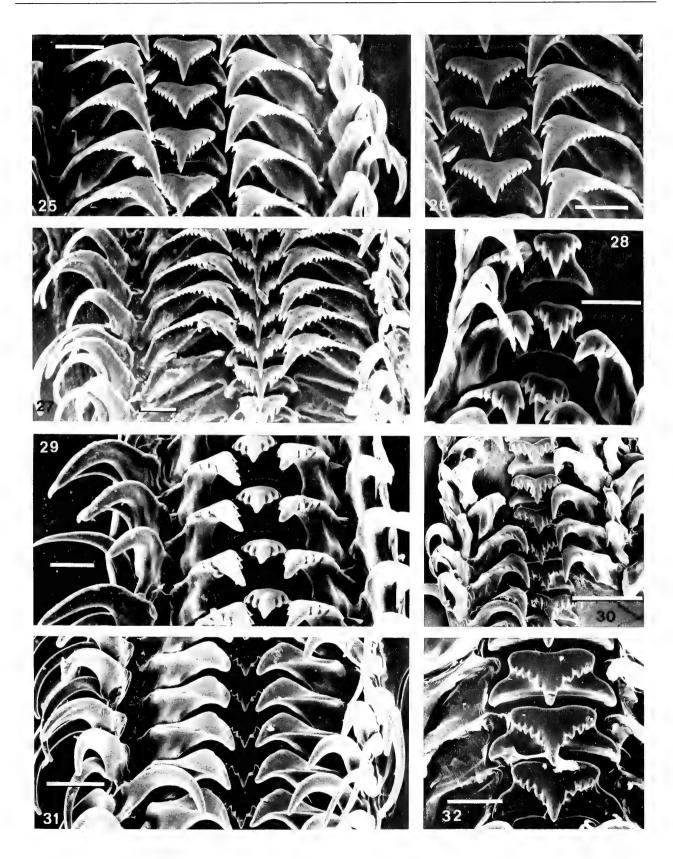
Figure 27. *Pisanianura breviaxe* (New Caledonia, MNHN). Scale line 50 μm.

Figure 28. *Sassia kampyla,* very young (New Zealand, NMNZ 9196). Scale line 25 μm.

Figure 29. *Sassia parkinsonia* (New South Wales, AMS C 50074). Scale line 50 μm.

Figure 30. *Ranella australasia,* planktonic larva (New South Wales, AMS C 147218). Scale line 25 μm.

Figures 31 and 32. *Ranella olearia* (the Azores, MNHN). Scale lines 200 and 100 μm.

Type material: *Hindsia grimaldii,* holotype in MOM; *Anura clathrata,* lectotype here selected, the specimen figured by Dautzenberg & Fischer (figs. 6, 8), in MOM.

Type localities: *Hindsia grimaldii,* Monaco Expeditions sta. 112, 38°39'N, 28°06'W, 1287 m (Azores); *Anura clathrata,* Monaco Expeditions sta. 719, 39°11'N, 29°06'W, 1600 m (Azores).

Material examined: The type material and: Talisman Expedition 1883, dragage 72, 25°39'N, 15°38'W, 882 m (off S Morocco), 1 shell (LOCARD, 1897:323), MNHN; Monaco Expeditions sta. 1116, 31°43'N, 10°47'W, 2165 m (off Morocco), 1 shell, MOM; Monaco Expeditions sta. 1236, 32°43'N, 17°03'W, 1500 m (S of Madeira), 1 shell, MOM; R/V *Vauban* sta. CH22, 12°27'S, 40°10'E, 680–700 m (off N Mozambique), coll. A. Crosnier, 1 specimen, MNHN; Biocal sta. DW51, 23°05'S, 167°45'E, 680–700 m (S New Caledonia), 2 specimens, MNHN.

Distribution: Only known from the material examined, northeastern Atlantic, southwestern Indian Ocean, and southwestern Pacific, in 700–2200 m.

Remarks: Despite the considerable geographical distribution, *Pisanianura grimaldii* shows little morphological variation, and we have no indication that the specimens from the northeastern Atlantic and the Indo-Pacific areas are not conspecific. Such a wide distribution seems to be well documented among the Tonnoidea (DELL & DANCE, 1963; SCHELTEMA, 1971, 1972; SCHELTEMA & WILLIAMS, 1983).

DAUTZENBERG & FISCHER (1906) enumerated several differences between *Pisanianura grimaldii* and *P. clathrata,* but direct comparison of the types proved them to be much smaller than appears from the text.

Pisanianura breviaxe (Kuroda & Habe, 1961)

(Figures 27, 123, 124, 153, 154)

Laminilabrum breviaxe Kuroda & Habe *in* HABE, 1961:36, app.:13, pl. 15, fig. 24 (Japanese edition); 1964:55, pl. 15, fig. 24 (English edition).

Type material: Lectotype, here selected, the shell figured

in references above, National Science Museum, Tokyo, Reg. No. 38611.

Type locality: Tosa Bay, Shikoku, Japan, 150–200 m.

Material examined: The lectotype; 1 paralectotype from Tosa Bay, USNM 658749; Biocal sta. DW36, 23°09'S, 167°11'E, 650–680 m, 1 specimen, MNHN; Biocal sta. CP52, 23°06'S, 167°47'E, 540–600 m (S New Caledonia), 1 specimen, MNHN; Fukura, Awaji, Japan, 1 shell, USNM 607197; Tosa Bay, Japan, 1 shell, USNM 617812; North of New Zealand, 28°39.5'S, 173°01'E, 837 m, 1 shell, A. Beu, NZGS (46 mm high).

Remarks: One of the New Caledonian specimens was found on a stem of a stalked crinoid, but no scar was visible and the animal fell off when preserved, which probably means that the association was fortuitous. There were no crinoid remains in the stomach of the dissected specimens.

Anatomy of *Pisanianura* (Figures 153, 154)

We have investigated the soft parts of the two recent species *Pisanianura grimaldii* and *P. breviaxe.* They are quite similar anatomically and we do not question that they belong to the same genus. The description below is based on *P. breviaxe*; differences from *P. grimaldii* are pointed out.

Most of the visceral mass was poorly preserved and not suitable for dissection. The foot is rather small and fleshy, with a conspicuous propodium, no median furrow on the ventral side, and no epipodial tentacles or flaps. The sides of the foot are strongly wrinkled close to the sole, with a constriction or furrow demarcating the smoother area above this furrow.

Operculum. See Figure 68.

The head is large and broad with two conical, blunt tentacles and large black eyes situated in lateral, basal bulges. There is no snout, only a thin membrane between the tentacles, over the proboscis opening. The presence of a penis is not known, because only females were examined.

The pallial cavity is rather deep, ca. 0.4 whorls, and spacious. The pallial edge is finely "crenulated," thick and muscular with a well-developed siphonal fold. A row of

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Explanation of Figures 33 to 40

Radulae of Ranellidae.

Figure 33. *Cymatium muricinum* (Hawaii, SMNH). Scale line 50 μm.

Figure 34. *Cymatium* sp., larva (Dana sta. 3940:Ib). Scale line 10 μm.
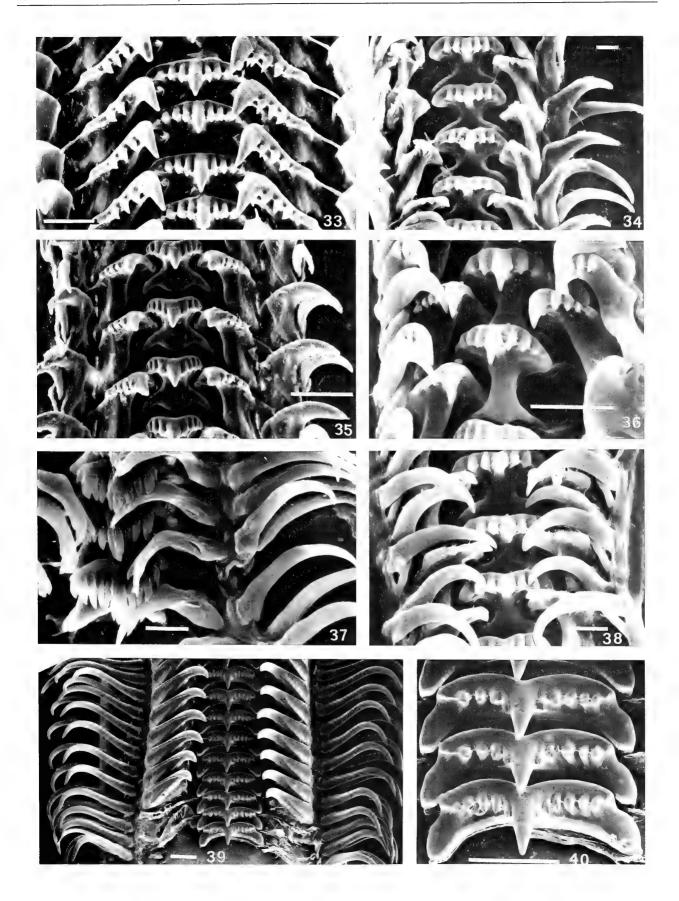
Figure 35. *Cabestana cutacea* (Mediterranean, SMNH). Scale line 50 μm.
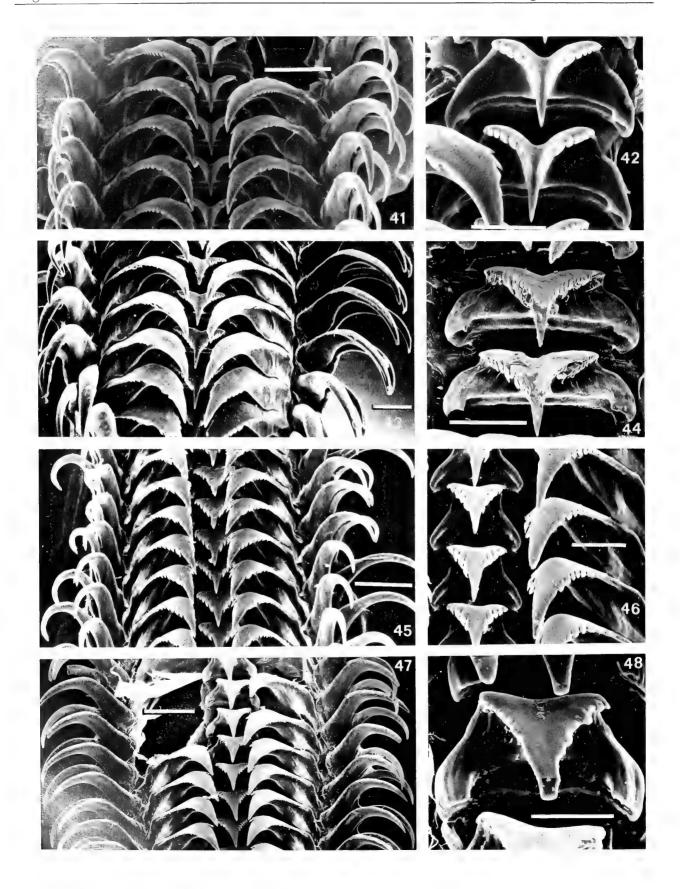
Figure 36. *Cymatium* sp., larva (Dana sta. 1253). Scale line 10 μm.

Figure 37. *Charonia* sp., larva (Dana sta. 1247). Scale line 10 μm.

Figure 38. *Cymatium* sp., larva (Dana sta. 3940:Ib). Scale line 10 μm.

Figures 39 and 40. *Charonia lampas* (SW Spain, SMNH). Scale lines 250 μm.

about 12 small papillae, parallel to the pallial edge, is present just in front of the gill. The osphradium is bipectinate, with the left lamellae half as long as the inner ones, and is situated along the central half of the gill. Its surface area corresponds to ¼ of that of the gill. No fine details were discernible because of poor preservation and a cover of tough mucus. The gill consists of 60–80 tongue-shaped leaflets, about 4 times as high as broad, and occupies the whole distance from the bottom of the pallial cavity to just to the right of the siphon. The hypobranchial gland is well developed and forms large quantities of mucus when placed in water (at least in preserved specimens).

The pallial oviduct is sausage-shaped, 2.5 times as long as broad, with a simple lumen. It is closed and opens through a pore ⅙ of its length from the distal end. There are six simple sac-shaped receptacula seminis situated dorsally along the posterior part of the oviduct, joining to a common duct leading towards the ventral, posterior part of the oviduct.

The rectum is almost hidden in the wall of the oviduct and opens just in front of the oviduct.

The proboscis sheath is broad, short, and thin-walled. The buccal mass is cylindrical, about twice as long as broad, connected to the anterior part of the proboscis sheath by a system of numerous thin retractor muscles. Two large retractor muscles attach to the posterior, ventral part of the buccal mass, pass through the nerve ring and attach in the floor of the cephalo-pedal haemocoel. The salivary glands are large, of normal tonnoid type (which was described in more detail by DAY, 1969), with a smaller, solid-looking part close to the thick ducts, which pass through the nerve ring, follow the laterodorsal sides of the buccal mass and become narrow before opening into the buccal cavity. The openings were not found. The prismatic jaws (Figure 55) are roughly semicircular and situated well in front of the radula.

Radula. Central tooth with a large median cusp and 5 or 6 smaller lateral denticles on each side. Lateral tooth thin, with a major cusp, two inner denticles, and external serrations. Marginals undifferentiated, simple, claw-shaped. Figures 25–27.

The nervous system is highly concentrated; the pleural ganglia are indiscernibly fused to the cerebral ones, which are short, broad, flat, and united by a short and broad commissure. The pedal connectives are long and slender, about 1.5 times the width of the two cerebral ganglia

together. The pedal commissure is short. The suboesophageal-pleural connective leaves the ventral side of the cerebro-pleural ganglion and runs along the floor of the body cavity to the suboesophageal ganglion, which is situated ventrally to the right cerebro-pleural ganglion, in the floor of the body cavity. A large nerve from the suboesophageal ganglion forms a zygoneury. The supraoesophageal ganglion is situated in a median position, between the two salivary glands; a zygoneury to the left cerebro-pleural ganglion was not verified.

Faecal pellets from the rectum contain sand, detritus, sponge spicules, remains of crustaceans, and calcareous particles or needles.

Pisanianura grimaldii differs mainly in having a more thin-walled proboscis sheath and a short, roughly globular buccal mass, a difference that, however, may be the result of contraction. Another difference is that the gill leaflets of *P. grimaldii* are semicircular instead of tongue-shaped.

Family LAUBIERINIDAE Warén & Bouchet, fam. nov.

(Figures 41–48, 56, 57, 71, 72, 96, 105–109, 128–131, 136–141, 155–162)

Diagnosis: Tonnoidea with a low-spired, fragile shell with poorly developed siphonal canal. Osphradium monopectinate, very large in the larva, of normal size in the adult. Proboscis short with large buccal mass.

Remarks: This new family is erected for the new genus *Laubierina*, and for a few species belonging to the genus *Akibumia* Kuroda & Habe, 1959, which previously have been classified (on the basis of shell and radula only) in the Trichotropidae. They differ from all other known Tonnoidea in having a fragile, more or less globular or weakly biconic, depressed shell with an indistinct siphonal canal, and in having a monopectinate osphradium (bipectinate in other adult Tonnoidea).

The shell provides little information about the relations of the **Laubierinidae** to other tonnoid families; unless typical salivary glands had been present, we should have been hesitant to include the **Laubierinidae** here. The radula, however, is similar to that of *Sassia* and *Pisanianura* in the Ranellidae. This is especially the case with the supporting ridge on the lateral tooth, which abuts the tooth in front, and the deeply excavated anterior base of the central tooth, which is equipped with basal denticles.

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Explanation of Figures 41 to 48

Radulae of **Laubierinidae**.

Figures 41 and 42. **Laubierina** sp., recently metamorphosed young, (Mozambique Channel, MNHN). Scale lines 100 and 50 μm.

Figures 43 and 44. **Laubierina peregrinator** (Mozambique Channel, MNHN). Scale lines 100 μm.

Figure 45. *Akibumia orientalis* (Japan, USNM). Scale line 100 μm.

Figure 46. *Akibumia orientalis* (New South Wales, AMS). Scale line 100 μm.

Figures 47 and 48. *Akibumia schepmani* (Queensland, AMS). Scale lines 100 and 50 μm.

The fact that the osphradium deviates from all other adult tonnoids in being monopectinate may be connected with the morphological or functional causes that have led to its hypertrophy in the larva (see "laubierinid larva sp. 1," page 79). This hypertrophy is caused by some biological trait during the larval or early post-larval life, because adult and half-grown specimens have an osphradium of normal size, although it is also here monopectinate. This may result from the late larva or early post-larva needing to use the osphradium for localization or recognition of females (see discussion, page 81) or for finding a rare or restricted habitat for settlement.

There may be further anatomical criteria beside those of the osphradium, but the knowledge of variation among other Tonnoidea is not detailed enough to allow further comparisons. One difference, however, is that no sexually mature specimens of Tonnoidea without post-larval growth are known, despite numerous late larvae having been investigated (SIMROTH, 1911; and own examinations of *Tonna* spp., *Bursa* sp., *Semicassis* sp., *Cymatium* spp., *Sassia* sp., *Ranella australasia*, and *Argobuccinum pustulosum tumidum* (Dunker, 1862)).

Laubierina Warén & Bouchet, gen. nov.

Type species: *Laubierina peregrinator* Warén & Bouchet, sp. nov.

Diagnosis: Larval shell large, multispiral, with strong reticulate sculpture and expanded outer lip formed soon before metamorphosis. Teleoconch fragile, biconic, low-spired with short, shallow siphonal canal. Periphery with strong keel; weaker spiral cords and dense sharp incremental lines below and above keel.

Remarks: A search of the literature and museum collections has failed to reveal any described species even remotely similar to *Laubierina peregrinator*.

The genus is named after Dr. L. Laubier (IFREMER, Paris), to whom we owe great thanks for his support of our work on deep-sea mollusks.

Laubierina peregrinator Warén & Bouchet, sp. nov.

(Figures 43, 44, 128, 129, 159–161)

Type material: Holotype in MNHN.

Type locality: Walvis sta. 13, 32°18′S, 13°16′E, 3550 m, off SW Africa.

Material examined: The holotype and: Benthedi sta. CH13, 12°13′S, 46°40′E, 2300–2500 m (Mozambique Channel), 2 specimens, MNHN.

Distribution: Known only from the material listed, the southeastern Atlantic, and southwestern Indian oceans, between 2300 and 3550 m.

Description: Shell thin, fragile, strongly depressed, somewhat angular. Larval shell and first teleoconch whorls dissolved or damaged in holotype. In other specimens, larval shell of 3.5 brown, convex whorls with symmetrically reticulate sculpture of axial and spiral ribs of about same strength. Axial ribs straight on the uppermost whorls, becoming somewhat flexuous and prosocline on last two whorls. Four spiral ribs visible above suture in middle whorls, of which lower one partially concealed by last whorl. Total height of larval shell 5.5 mm, of which 3.6 mm visible above suture. Teleoconch with strong keel, situated just above suture and giving impression of strongly channelled suture. Whorls slightly convex above and below keel. Sculpture of sharp, regular incremental lines and stronger spiral ridges, 8 on first teleoconch whorl and 12 on last whorl, above keel; on body whorl below keel, ca. 20 ridges. Outer lip thin, regularly convex. Inner lip a thin parietal callus, forming narrow umbilicus. Siphonal canal short and open. Shell white, thin, covered by brownish beige periostracum with numerous axial lamellae parallel to growth lines.

Dimensions. Height of holotype 18.8 mm, diameter 19.5 mm, height of aperture 14.5 mm, breadth 11 mm.

Remarks: No gastropod known to us can be confused with *Laubierina peregrinator* except perhaps a young *Modulus* Gray, 1842 (Modulidae, Cerithioidea), but the species of that genus have a much more solid, strongly sculptured shell, and a columellar denticle.

The name *peregrinator* means migrant, alluding to a supposed long planktonic life.

In addition to the type species we have examined several young specimens and larval shells that we consider to belong to *Laubierina*, but they are too young to be determined accurately at the specific level.

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Explanation of Figures 49 to 57

Jaws of Tonnoidea. Scale lines 250 μm.

Figure 49. *Tonna allium* (Sumatra, SMNH).

Figure 50. *Oocorys sulcata* (off Portugal, MNHN).

Figure 51. *Galeodea echinophora* (Mediterranean, SMNH).

Figure 52. *Argobuccinum pustulosum* (New Zealand, NMNZ).
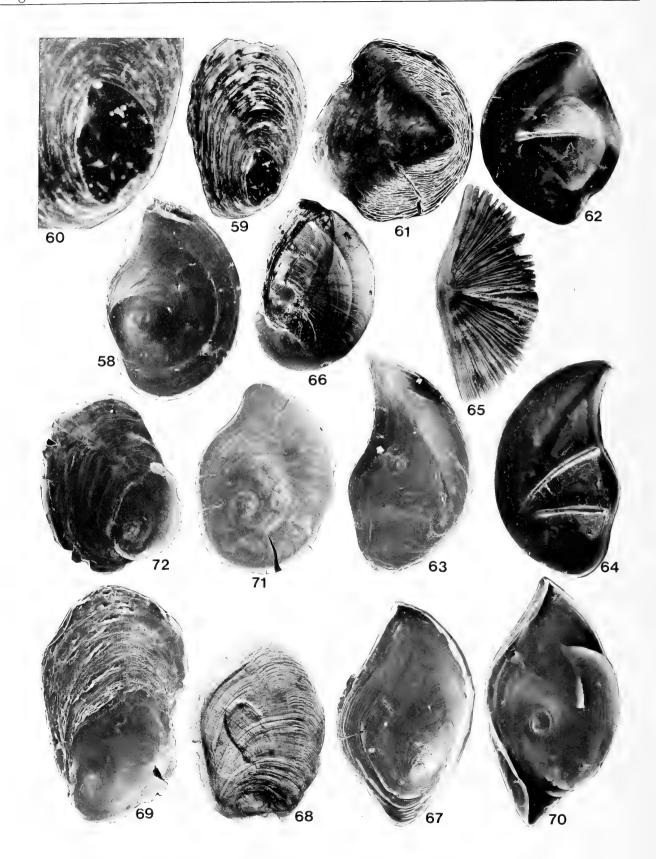
Figure 53. *Fusitriton magellanicus* (SMNH).

Figure 54. *Cabestana cutacea* (Sicily, SMNH).

Figure 55. *Pisanianura grimaldii* (New Caledonia, MNHN).

Figure 56. *Laubierina* sp., recently metamophosed benthic stage (Mozambique Channel, MNHN).

Figure 57. *Akibumia orientalis* (New South Wales, AMS).

Laubierina sp. A

R/V *Jean Charcot*, 1969, Madere sta. 13, 32°34′N, 17°07′W, 1970 m, 1 shell with ⅔ of a teleoconch whorl, MNHN. See Figure 106.

Cancap 2, Canaries, sta. 2.067, 27°58′N, 14°12′W, 2067 m, 2 larval shells, no post-larval growth, RMNH.

Biacores sta. 195, 37°56′N, 24°49.5′W, 1700–1776 m, 1 shell with no post-larval growth, MNHN. See Figures 105, 107, and 108.

Gulf of Mexico, 21°35′N, 96°54.6′W, 937 m, 1 young shell with ⅔ of a teleoconch whorl, MNHN. See Figures 130 and 131.

These specimens may represent a single species; the two specimens with post-larval growth certainly do.

Laubierina sp. B

Biocal sta. DW48, 23°00′S, 167°29′E, 775 m, 1 young shell with 1.4 post-larval whorls, MNHN. See Figure 96.

Off Broken Bay, New South Wales, 1000 m, 1 shell without post-larval growth, AMS C 150186.

NZOI sta. P941, 41°15.2′S, 167°07.2′E, 1457–1463 m, 1 shell without post-larval growth, NZOI.

These three specimens probably represent a third species, differing by the sculpture of protoconch II, which is more dense than in the North Atlantic specimens.

Anatomy of *Laubierina* (Figures 159–161)

The description is based on two females of *Laubierina peregrinator*. The visceral mass was not extracted because of the risk of damaging the shell.

The foot is small, strongly contracted and muscular, blunt anteriorly, and rounded posteriorly. The propodium is well developed. The wrinkled, lower side of the foot is demarcated by a distinct furrow. There are no epipodial tentacles or folds.

Operculum. Similar to that of *Pisanianura* (Figure 68), but the apical part is more corroded.

The head is large and broad. The tentacles are slender and cylindrical with the eyes in large latero-basal bulges. The presence of a penis is not known, because only females were examined.

The pallial cavity is rather shallow, occupying 0.3 whorls. The pallial edge is simple and slightly thickened. A poorly developed siphon is indicated by the left corner of the pallial edge being more muscular. The osphradium is large, about ⅔ of the length of the gill, monopectinate, and has the leaflets directed towards the gill axis. The gill has about 85 low, triangular leaflets, and the free corner of each leaflet is drawn out into a tongue-shaped process.

The pallial oviduct is simple, closed, and sausage-shaped. A receptaculum seminis was not found. The rectum runs along the pallial oviduct in the pallial roof.

The proboscis sheath is short, thin-walled, and broad, and is evidently fully everted in one of the specimens (Figure 152). The buccal mass is large, globular, solid, and muscular. The salivary glands are large, of normal tonnoid type, and with the ducts passing through the nerve ring. The jaws were not examined.

Radula. Central tooth with a daggerlike median cusp and 8 or 9 lateral denticles. Lateral teeth fairly solid and robust and with 2 inner denticles, a median cusp, and a serrated external margin. Marginal teeth undifferentiated, simple, claw-shaped. Figures 43 and 44.

The anterior oesophagus is thin-walled and spacious; the posterior oesophagus forms an oesophageal gland, which is smaller than in other tonnoids.

The cerebral ganglia are large, connected by a slender commissure and well separated from the pleural ganglia, which are connected by short connectives. Two major nerve stems arise from the anterior edge of the cerebral ganglia and innervate the proboscis sheath; a third nerve leaves the anterior ventral side of the cerebral ganglion and forms the buccal connective; a fourth nerve leaving the lateral part leads to the tentacle. The suboesophageal ganglion is situated shortly to the right of behind and below the corresponding cerebral ganglion; the suboesophageal ganglion

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Explanation of Figures 58 to 72

Opercula of Tonnoidea.

Figure 58. *Bursa* sp., larva (off Brasil, MNHN), max. diam. 1.33 mm.

Figures 59 and 60. *Bursa* sp., adult (Gilbert Id., SMNH), max. diam. 5.5 mm, and detail of the nucleus.

Figures 61 and 62. *Tonna* sp., larva (off SE South Africa), max. diam. 3.2 and 3.6 mm respectively.

Figures 63 and 64. *Semicassis* sp. aff. *granulatum*, larva (Dana sta. 1353), max. diam. 1.8 and 2.0 mm respectively.

Figure 65. *Semicassis granulatum* (no loc., SMNH), max. diam. 37 mm.

Figure 66. *Oocorys abyssorum* (SE Atlantic, MNHN), max. diam. 11.6 mm.

Figure 67. *Charonia* sp., larva (Dana sta. 1247:II), max. diam. 2.3 mm.
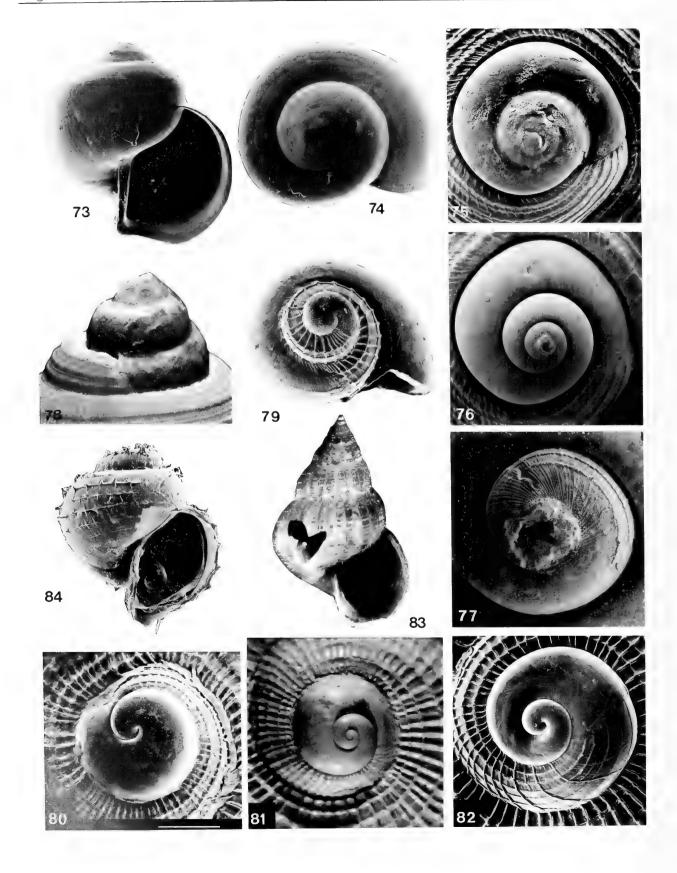
Figure 68. *Pisanianura grimaldii* (New Caledonia, MNHN), max. diam. 4.8 mm.

Figure 69. *Argobuccinum pustulosum* (New Zealand, NMNZ), very young specimen, max. diam. 3.7 mm.

Figure 70. *Cymatium* sp., larva (Dana sta. 3940:Ia), max. diam. 1.8 mm.

Figure 71. *Laubierina* sp., larva (Mozambique Channel, MNHN), max. diam. 2.9 mm.

Figure 72. *Akibumia orientalis* (Japan, USNM), max. diam. 2.9 mm.

is connected to the right pleural ganglion by a solid nerve, and to the left pleural ganglion via a long slender connective. The supraoesophageal ganglion is situated to the left of and behind the left pleural ganglion; no zygoneury was found, only a connection to the right pleural ganglion. The buccal ganglia are large, situated ventrally at the posterior part of the buccal mass.

The rectum contained radiolarian tests, fragments of crustaceans, scattered sponge spicules, polychaete bristles, unidentified organic matter, scattered diatom skeletons and very few mineral particles.

Akibumia Kuroda & Habe, 1959

Akibumia Kuroda & Habe *in* Kuroda, 1958:pl. 20, fig. 4. (Not available, ICZN Article 13a, e.)
Akibumia Kuroda & Habe *in* Kuroda, 1959:317.

Type species: *Akibumia flexibilis* Kuroda & Habe, 1959, by monotypy.

Remarks: Beside the three species here included in the genus, Habe (1962) described *Akibumia reticulata* from Honshu, Japan. We have examined the holotype (Figure 83) and conclude that it is an epitoniid as also is indicated by it being found attached to coelenterates (Habe, 1962). It may provisionally be classified in *Epitonium*.

Habe (1962:74) also suggested that *Fossarus cereus* Watson, 1880, from 2580 m, off northeastern Australia is related to *Akibumia*. He had evidently overlooked Pelseneer's (1888) note on this species, based on the soft parts of the holotype, which Pelseneer placed in the "Pleurotomidae" (=Turridae). Pelseneer, however, did not describe the soft parts, but rather remarked only that the animal lacks eyes and "cervical lobes" (=the lobes between the tentacles?) and is therefore probably not a *Fossarus*. We have examined the holotype in BMNH and are uncertain about its systematic position as all the apical parts are corroded; however, the absence of eyes and presence

of a snout in Watson's figure (1886:pl. 43, fig. 4d) are good indications that it does not belong to the **Laubierinidae**. Golikov & Starobogatov (1986) referred *Fossarus cereus* to *Conradia* (*Gottiana*) [*sic*!; should be *Gottonia* A. Adams, 1863], together with a new species, described as *Conradia minuta* Golikov & Starobogatov, 1986, from the North Pacific. Judging from the figure, the new species actually is a veliger larva of a ranellid, whereas both *Gottonia* and *Conradia* are based on type species belonging to the Trochoidea (Warén, examination of type material of the type species).

Akibumia orientalis (Schepman, 1909)

(Figures 45, 46, 57, 72, 136–138, 157, 158)

Trichotropis orientalis Schepman, 1909:176, pl. 12, fig. 2.

Type material: Holotype ZMA 3.02.041.

Type locality: Siboga Expedition sta. 211, 05°41′S, 120°46′E, 1158 m (Banda Sea).

Material examined: The holotype and: Albatross Expedition sta. 4919, 30°34′N, 129°19′E, Kagoshima Gulf, Japan, 805 m, 1 female, USNM 206835; 33°36′S, 152°05′E, 1106–1143 m (off Sydney, Australia) 1 female, AMS C 150223; Three Kings Rise, New Zealand, 31°19.9′S, 173°05.1′E, 1563–1570 m, 1 shell, NZOI.

Distribution: Known only from the material examined, western Pacific in 805–1570 m.

Remarks: *Akibumia orientalis* is well characterized by the strong spiral keels. We do not know any Recent gastropod that even resembles it. In addition to this, there is a distinct sculpture of strong, close-set incremental lines and finer spiral ribs, which is especially strong on the keels. The specimen from off Sydney was dissected and the results are presented below. The Japanese female had been dried and could not be used for detailed examination.

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Explanation of Figures 73 to 84

Larval shells of Tonnidae and Ficidae.

Figures 73 and 74. *Tonna* sp., larvae (off SE South Africa, SMNH), height 4.5 mm, diameter 3.6 mm.

Figure 75. *Tonna galea,* apical view with complete protoconch (Malta, SMNH), diameter of the larval shell 3.2 mm.

Figure 76. *Tonna galea,* apical view; the periostracum of the protoconch has been dissolved in bleach and the calcareous internal mould of the protoconch, with disjunct whorls, is now visible (Brasil, SMNH), diameter of the larval shell 3.3 mm.

Figure 77. Same specimen as Figure 76, close-up view of protoconch I and early part of protoconch II, width of photo 1.0 mm.

Figure 78. *Eudolium crosseanum,* side view of apex with complete protoconch (Azores, MNHN), height of larval shell 3.1 mm.
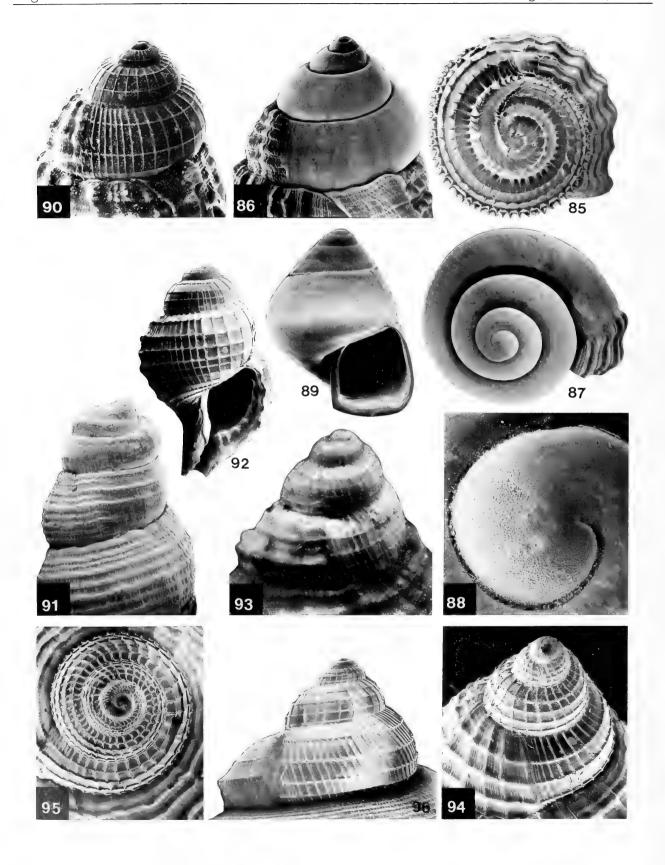
Figure 79. Same specimen as Figure 78, protoconch I and initial part of protoconch II; the periostracum has been removed in bleach; max. diam. 1.0 mm.

Figure 80. *Ficus communis* (Florida, SMNH). Scale line 250 μm.

Figure 81. *Ficus conditus* (Lower Miocene, France), diameter of the protoconch 1.8 mm.

Figure 82. *Ficus* sp. (Philippines, MNHN), diameter of the protoconch 2.2 mm.

Figure 83. *Akibumia reticulata,* holotype, height 7.55 mm.

Figure 84. *Distorsio* sp. (Philippines, MNHN), larval shell with traces of post-larval growth, diameter 1.2 mm.

Akibumia flexibilis Kuroda & Habe, 1959

(Figures 109, 140, 141)

Akibumia flexibilis Kuroda & Habe in KURODA, 1958:pl. 20, fig. 4 (not available, ICZN Article 13a, e).
Akibumia flexibilis Kuroda & Habe in KURODA, 1959:317.

Type material: Two syntypes in Kuroda's private collection; the shell figured as "holotype" by ANONYMOUS, 1986: pl. 17, figs. 3–5, is not to be considered a lectotype according to ICZN art. 74(b) because a nomenclatural act published anonymously after 1950 is not available (ICZN art. 14).

Type locality: "Deep bottom off Tosa, Shikoku, Japan."

Material examined: The type material and: 06°52'S, 39°54'E, off Tanzania, 1 shell, USNM 718939; Tosa, Japan, 270 m, 1 shell, ANSP 234711.

Remarks: We are not convinced that this species can be distinguished from *Akibumia schepmani,* although the spire gives an impression of being lower in that species. This difference is probably caused by the larval shell being almost completely eroded away in the holotype of *A. schepmani.* The lack of material, in combination with the presumed wide distribution, makes synonymization unsafe and we have preferred to keep the two species separate.

Akibumia schepmani Habe, 1962

(Figures 47, 48, 139, 155, 156)

Akibumia schepmani HABE, 1962:74.

Type material: Holotype ZMA 3.62.001.

Type locality: Siboga Expedition sta. 211, 05°41'S, 120°46'E, 1158 m (Banda Sea).

Material examined: The holotype and: 28°01'S, 153°59'E, 550 m (off Gold Coast, southern Queensland), coll. K. Graham, 1 specimen, AMS 150192.

Distribution: Known only from the two specimens examined.

Remarks: The name *Akibumia schepmani* is based on SCHEPMAN's (1909:177, pl. 12, fig. 3; pl. 16, fig. 3) description and figures of an unnamed gastropod of doubtful family position. Schepman had two specimens; we have regarded the figured shell as the holotype; the second specimen was probably destroyed by Schepman when he extracted the radula.

We find it remarkable that the Siboga Expedition obtained two species of this otherwise rare genus in the same dredge-haul, but other gastropods obtained in the same haul give no indication of any special character of the biotope.

Anatomy of *Akibumia* (Figures 155–158)

The description is based on *Akibumia orientalis*; the differences from *A. schepmani* are pointed out below. Most of the visceral mass was poorly preserved and unsuitable for dissection, but it consists of about 3.5 whorls, mainly occupied by the ovary.

The foot is small, strongly contracted, and muscular, without a median furrow or any epipodial appendages, but with a distinct propodium. The sides of the foot are strongly wrinkled close to the ventral edge and with a furrow demarcating this area from the smoother, higher parts.

Operculum. Fairly solid, yellowish brown, fan-shaped, with the larval operculum remaining apically. Figure 72.

The head is large and broad with short, stout (contracted) tentacles with the eyes situated in large latero-basal bulges. The snout is short and inconspicuous, and consists mainly of a thin membrane between the tentacles, covering the proboscis opening. The penis is not known, as only females were examined.

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Explanation of Figures 85 to 96

Larval shells of Ranellidae and **Laubierinidae**.

Figure 85. *Fusitriton magellanicus* (New Zealand, NMNZ), young post-larva with periostracum of the larval shell intact, diameter 3.2 mm.

Figure 86. *Argobuccinum pustulosum* (New Zealand, NMNZ), internal mould of larval shell obtained by removal of the periostracum (see text for explanation); note the slightly disjunct whorls; width of photo 4.2 mm.

Figure 87. *Ranella olearia* (SW Europe, MNHN), very young post-larva with internal mould of larval shell with disjunct whorls, diameter 3.6 mm.

Figure 88. Same specimen as Figure 87; close-up view of protoconch I, diameter 560 µm.

Figure 89. *Ranella australasia* (plankton off Sydney, AMS), height 3.8 mm.

Figure 90. *Sassia raulini* (Miocene of France), width of photo 3.4 mm.

Figure 91. *Sassia textilis* (Miocene of Victoria, AMS), height 4.3 mm.
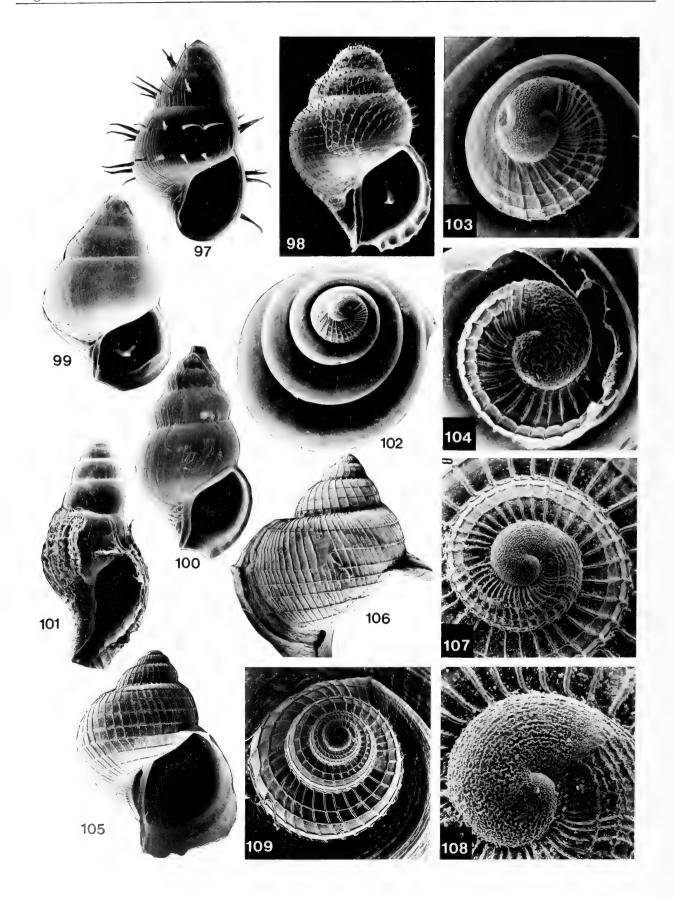
Figure 92. *Sassia remensa* (Queensland, AMS), height 3.2 mm.

Figure 93. *Pisanianura inflata* (Pliocene of Italy), height of the protoconch 2.2 mm.

Figure 94. *Pisanianura grimaldii* (Madagascar, MNHN), width of photo 3.4 mm.

Figure 95. *Pisanianura grimaldii* (New Caledonia, MNHN), diameter of larval shell 2.3 mm.

Figure 96. **Laubierina** sp. (New Caledonia, MNHN), height of larval shell 3.0 mm.

The pallial cavity is shallow, occupying 0.25 whorls, and spacious. The pallial edge is slightly thickened in *Akibumia orientalis*, with indistinct internal crenulation. The right corner of the pallial edge (in *A. schepmani* and *A. orientalis,* both females) is equipped with a thin, muscular skin-fold, hanging down as a protective curtain, just in front of the pallial oviduct and the rectum. This skin-fold starts 2 mm in front of the left edge of the anus (0.5 mm behind the pallial edge) from the roof, grows higher towards the right, to a height of about 2 mm just in front of the right edge of the oviduct, where it forms a 90° turn backwards and becomes gradually lower. The siphonal canal is only indistinctly indicated by a more muscular area around the left corner of the pallial edge. The osphradium is monopectinate, with about 40 leaflets covering most of the area between its axis and the gill axis. The axis of the osphradium runs parallel to the central part of the gill axis and is half as long. The gill occupies almost the entire distance from the innermost part of the pallial cavity to the pallial edge and consists of about 75 low, triangular leaflets of which the free corner is drawn out into a tongue-shaped projection, measuring 2.0 × 1.2 mm (high) in the central parts of the gill.

The pallial oviduct is closed and sausage-shaped, 1.5 times as long as broad and with a simple flat cavity. The opening was not found. A group of seven simple, sac-shaped receptacula seminis is situated just behind the proximal end of the oviduct, and the receptacula open to a single duct leading towards the oviduct. The rectum runs along the left side of the oviduct and opens on a small papilla, just behind the distal end of the oviduct.

The proboscis sheath is short and thick-walled. The buccal mass is long and cylindrical, almost twice as long as broad, and is connected to the proboscis sheath along its sides by numerous fine muscle fibres. A large, solid muscle is attached to each posterior side and connects to the floor of the body cavity shortly behind the nerve ring. (These seem to be the main muscles for retraction of the proboscis.) The salivary glands are large and occupy most of the space of the body cavity behind the nerve ring. They consist of a large, distal, almost transparent part (accessory salivary gland) and a more solid, proximal part. The right gland is situated in front of and above the left one. The ducts are thick-walled, pass through the nerve ring, run dorsally on the buccal mass, and open rather far forwards. The anterior oesophagus is spacious and thin-walled and leads to a large oesophageal gland. The jaws (Figure 57) are large, rounded, and situated well in front of the radula.

Radula. Short, 40–50 transversal rows. Figures 45–48.

The nervous system is highly concentrated. The pleural ganglia are visible as bulges from the cerebral ones. The cerebral commissure is slightly more slender than the ganglia it connects. Three major nerves emerge from the anterior edge of the cerebral ganglia and innervate the proboscis; the most lateral one of these leads to the buccal mass, the inner one innervates the area around the true mouth, and the central one innervates the proboscis sheath. One large lateral nerve from each cerebral ganglion innervates the corresponding tentacle. The suboesophageal ganglion is situated shortly behind and below the right cerebral ganglion and is connected to the two pleural ganglia. The supraoesophageal ganglion is situated further posteriorly in the cavity, and is connected to the right pleural ganglion via a long connective and to the left pleural ganglion via a zygoneury to the osphradial nerve.

Akibumia schepmani differs mainly in having a slightly deeper pallial cavity, occupying about 0.4 whorls; in having long and slender tentacles; in having about 75 leaflets in the gill and 45 in the osphradium; and by having only five receptacula seminis and a more slender pallial oviduct, about 2.5 times as long as broad. The only specimen available was a female.

Undetermined Laubierinid Larvae

Larva Species 1

(Figures 41, 42, 56, 71, 162)

Material examined: One dried specimen with crushed shell in sample of benthic material, Benthedi 1977 sta. 87,

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Explanation of Figures 97 to 109

Larval shells of Ranellidae and **Laubierinidae**.

Figure 97. *Cymatium* sp., young larva (Dana sta. 1337), height 1.85 mm.

Figure 98. *Cymatium* sp., larva (Dana sta. 1253), height 3.6 mm.

Figure 99. *Charonia* sp., larva (Dana sta. 1247), height 4.2 mm.

Figure 100. *Cymatium* sp., larva (Dana sta. 3940:Ia), height 4.1 mm.

Figure 101. *Cymatium problematicum* (Canaries, SMNH), young post-larva, height 5.6 mm.
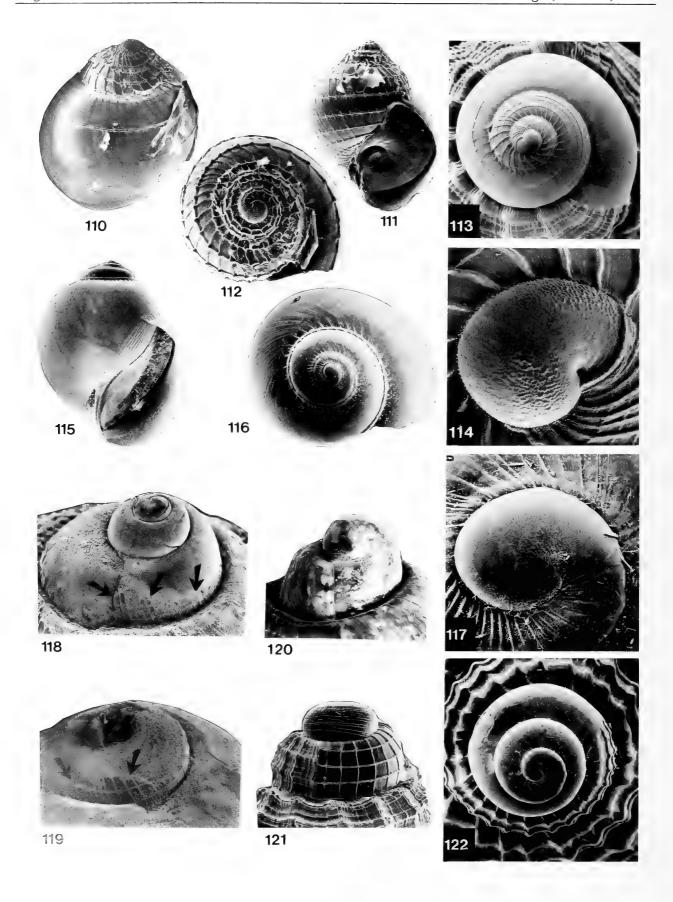
Figures 102 and 103. *Cymatium* sp. (Madeira, SMNH), post-metamorphic larva; the periostracum has been removed; max. diam. 1.85 mm, diameter of protoconch I, 315 μm.

Figure 104. *Cymatium* sp., same larva as Figure 98; the larval shell is seen from inside and shows the periostracal mould of the sculpture of the young calcified larval shell; breadth of field 0.5 mm.

Figures 105, 107, and 108. **Laubierina** sp. (Azores, MNHN), larval shell, height 3.6 mm; detail of the protoconch I and initial part of protoconch II; breadth of field 0.75 mm (Figure 107), diameter of protoconch I, 300 μm (Figure 108).

Figure 106. **Laubierina** sp. (Madeira, MNHN), young benthic specimen with less that one post-larval whorl, height of the protoconch 5.4 mm.

Figure 109. *Akibumia flexibilis* (Japan, ANSP), width of photo 3.1 mm.

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11°44'S, 47°35'E, 3716 m (northern Mozambique Channel), MNHN.

Remarks: This single specimen was badly broken, and the generic identification is uncertain. Several shell fragments were still attached to the soft parts, showing a sculpture of square and rectangular surfaces defined by sharp ridges. The radula (Figures 41, 42), which is similar to that of adult *Laubierina* and *Akibumia,* has a small denticle at the lateral part of the base of the central tooth, similar to *Pisanianura.* However, for several other Tonnoidea, minor changes in radular morphology may take place during the growth from larva to adult.

We consider that the characteristic protoconch sculpture and the size, at least 5 mm, in combination with the monopectinate osphradium, the radula, and the operculum, make the identification reliable to family level.

Description: The larva (Figure 162) was soaked in 1% formalin with detergent added.

The foot is large, flat, blunt anteriorly, and rounded posteriorly, with a wrinkled zone just above the sole and a demarcating furrow above the wrinkled zone. The propodium is well developed. There are no pedal appendages.

Operculum. See Figure 71.

The head is large and broad with small, cylindrical tentacles. The huge eyes, twice the diameter of the tentacles, are attached laterally to the basal part of the tentacle. There is no snout, only a thin membrane between the tentacles covering the proboscis opening. The penis is long, simply finger-shaped and slender, reaching all the way back to the bottom of the pallial cavity, where it curves 180° and lies folded double for ¼ of its length. The pallial seminal furrow is open and runs along the right side of the pallial cavity to the left, bordered by a swollen rim, possibly a prostate; the furrow then curves to the left and reaches the penis, where it continues open along the dorsal side, up to the tip.

The pallial edge is simple and muscular, with a thickened left corner equipped with two ridges, which possibly function as a siphon. The osphradium is huge and monopectinate, with about 35 leaflets that are twice as high as broad and directed towards the gill. They cover ⅚ of the distance from the bottom of the pallial cavity to the pallial edge and cover about ⅔ of the total inner surface of the pallial skirt. The gill is much smaller, is situated along the posterior ⅓ of the osphradium, and corresponds to ⅓ of its width. The gill has about 10 low, triangular leaflets. The rectum opens far back in the pallial cavity, at about ⅓ of its depth from the pallial edge.

The buccal mass was partly everted and shows the true mouth with a pair of lateral jaws and a large glandular-looking bulge at each side of the mouth. These are presumed to be reduced velar lobes.

Radula. See Figures 41 and 42.

The visceral mass consists of 1.75 whorls, of which the stomach, kidney, and heart occupy the basal 0.2 whorls and the digestive gland the following 0.5. The remaining part is completely filled by the testis and the vesicula seminalis.

Larva Species 2

Material examined: Discovery sta. 10141, 24°34'N, 19°41'W, 3460–3470 m, 1 young specimen without postlarval growth, 4.2 mm.

Description: The head-foot is similar to that of the larva described above, except that the specimen lacks developed reproductive organs. Glandular pads similar to those in Figure 162, supposed to be the remains of the velum, were present. Osphradium monopectinate.

The rectum and the stomach contained some mineral particles and unidentified organic matter.

Reproductive Biology of the **Laubierinidae**

The laubierinid larva sp. 1, taken in a bottom sample from 3716 m depth, off Madagascar, is remarkable for the presence of a penis and a visceral mass full of sperm. This indicates that the specimen was ready to mate before postlarval growth had begun. This has not been known for tonnoid or other meroplanktonic gastropod larvae.

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Explanation of Figures 110 to 122

Larval shells of Ranellidae, Bursidae, and Cassidae.

Figures 110 to 112. *Bursa* sp., young larvae (off Brasil, MNHN), heights 1.3 mm and 1.45 mm, and diameter 1.8 mm.

Figures 113 and 114. *Bufonaria marginata* (West Africa, MNHN), protoconch in apical view; diameter of protoconch II, 2.4 mm; of protoconch I, 330 µm.

Figures 115 to 117. *Cypraecassis testiculus* (Dana sta. 1286), height 3.1 mm (Figure 115), diameter 2.4 mm (Figure 116), diameter of protoconch I, 270 µm (Figure 117).
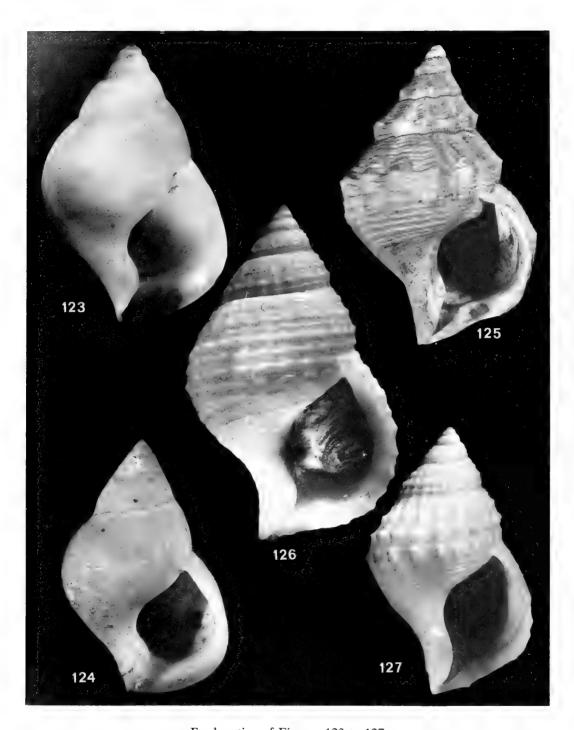
Figure 118. *Oocorys umbilicata,* apex, width of picture 2.4 mm. Note remains of protoconch II, indicated by arrows.

Figure 119. *Oocorys bartschi,* apex, width of picture 1.2 mm. Note remains of sculpture of protoconch II, indicated by arrows.

Figure 120. *Galeodea echinophora,* apex, height of larval shell 1.0 mm.

Figure 121. *Distorsionella lewisi,* apex, height of larval shell 1.1 mm.

Figure 122. *Distorsio* sp. (New Caledonia, MNHN), diameter of larval shell 1.07 mm.

Explanation of Figures 123 to 127

Pisanianura species.

Figure 123. *P. breviaxe* (New Caledonia), 15.5 mm.

Figure 124. *P. breviaxe,* holotype, 20.7 mm.

Figure 125. *P. inflata* (Pliocene, Italy), 24.4 mm.

Figure 126. *P. grimaldii,* holotype, 27.6 mm.

Figure 127. *P. grimaldii* (off Madagascar, MNHN), 23.0 mm.

In connection with this sexually mature male larva, it is of interest to note that out of the six adult specimens of **Laubierinidae** that have been examined, all proved to be females (probability 1/64 assuming a 1:1 sex ratio). This gives reason to speculate that the species of **Laubierinidae** are protandrous hermaphrodites with neotenic males. No structure was found in the larva that could be a receptaculum seminis or bursa copulatrix, and therefore it seems unlikely that copulation takes place in the planktonic phase.

Family FICIDAE Meek, 1864

(Figures 1–4, 80–82, 132–135, 148, 149)

There is no good description of the anatomy of *Ficus* Röding, 1798, but scattered information is present in several papers, and does not conform well with a position in the Tonnoidea. The animal has been figured several times (ÖRSTED, 1850; H. & A. ADAMS, 1853–1858; KEEN, 1971; WILSON & GILLETT, 1971; ARAKAWA & HAYASHI, 1972). The pallial edge is greatly enlarged and forms a fold surrounding the shell, much more so in *F. ventricosa* (Sowerby, 1825), where it is so wide that it extends over the foot; at the same time the foot is reduced (ÖRSTED, 1850), thus giving a configuration similar to *Lamellaria* Montagu, 1815 (Lamellarioidea). The head part of the head-foot is small and slender, more so than in the Bursidae, where it is the smallest in the superfamily. The seminal duct is closed throughout its way to the penis (BOSS, 1982) (open in other Tonnoidea, except some species of *Tutufa,* Bursidae; THIELE, 1929; BEU, 1981; and own observations). The proboscis is long and slender and lies coiled in the sheath, as in the Personidae, but in the Ficidae this occupies a large part of the cephalo-pedal haemocoel. The buccal mass is small, in preserved specimens not broader than the anterior oesophagus, and equipped with a pair of large jaws. The salivary glands are small and inconspicuous in *Ficus* (THIELE, 1929; AMADRUT, 1898; pers. obs.: 1.2 × 0.7 mm in a 40-mm *F. subintermedia*), situated far back in the body cavity and connected via long, slender ducts,

whereas in other Tonnoidea they are complex and large. To what extent these differences are connected to differences in feeding is uncertain. The only published information about the diet of *Ficus* is that it feeds on sea urchins (WILSON & GILLETT, 1971), whereas of four specimens of *Ficus subintermedia* we examined, two had empty alimentary canals, one had remains of a polychaete, and one had a long tube-shaped cuticle in the rectum.

This information about the anatomy and feeding biology of *Ficus* agrees well with the new information about *Thalassocyon* presented below and confirms that BEU's (1969) transfer of *Thalassocyon* to Ficidae was justified.

This anatomical information also distinguishes the Ficidae from all other families of the Tonnoidea, but does not necessarily indicate that the Ficidae has to be separated from the superfamily. However, it can be assumed that they branched off before the hypertrophied salivary glands of other Tonnoidea were developed. It is more difficult to imagine that the salivary glands have been reduced. Fossil evidence also indicates that the Ficidae, morphologically similar to Recent *Ficus*, already existed in the Upper Cretaceous (WENZ, 1941).

A planktonic larva of *Ficus* has never been reported, but some information about the larval development of *Ficus* was given (in Japanese) by AMIO (1963), who figured egg capsules. WRIGLEY (1929) described the apical whorls of several species of *Ficopsis* Conrad, 1866, and *Ficus* from British Cenozoic deposits, and SMITH (1907) described those of some Recent and Cenozoic species. Interpretation of protoconchs in the Ficidae is presently impossible because there are no known reference cases. The calcified larval shell is smooth, except on the last part (Figures 80–82) (in Tonnoidea with calcified larval shell, protoconch I is usually sculptured with pits and minute tubercles; protoconch II is often with at least the initial part reticulated). The limits between protoconch I and II and between protoconch II and the teleoconch are indistinct, but the protoconch of *Ficus communis* (SMITH, 1945:pl. 1, figs. 1, 2, and this paper Figure 80) seems to indicate non-

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Explanation of Figures 128 to 135

Shells of *Laubierina* (Figures 128 to 131) and *Thalassocyon* (Figures 132 to 135).

Figure 128. *L. peregrinator,* holotype, diameter 19 mm.

Figure 129. *L. peregrinator,* paratype (not adult), diameter 13.8 mm.

Figures 130 and 131. *L.* sp. (Caribbean, MNHN), height 13.2 mm.

Figure 132. *T. bonus,* holotype, 45 mm.

Figure 133. *T. bonus* (NMNZ 35293), diameter 12.6 mm.

Figure 134. *T. bonus* (NMNZ 75253), height 76 mm.

Figure 135. *T. bonus* (Amsterdam Id., MNHN), 28 mm.

Explanation of Figures 136 to 141
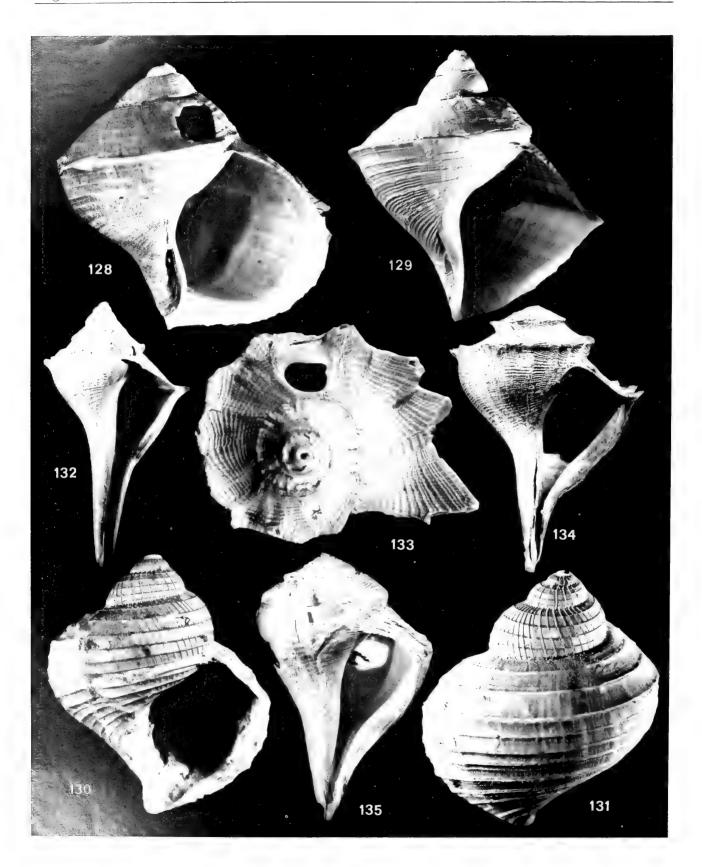
Shells of *Akibumia.*

Figure 136. *A. orientalis* (Japan, USNM), diameter 9.25 mm.
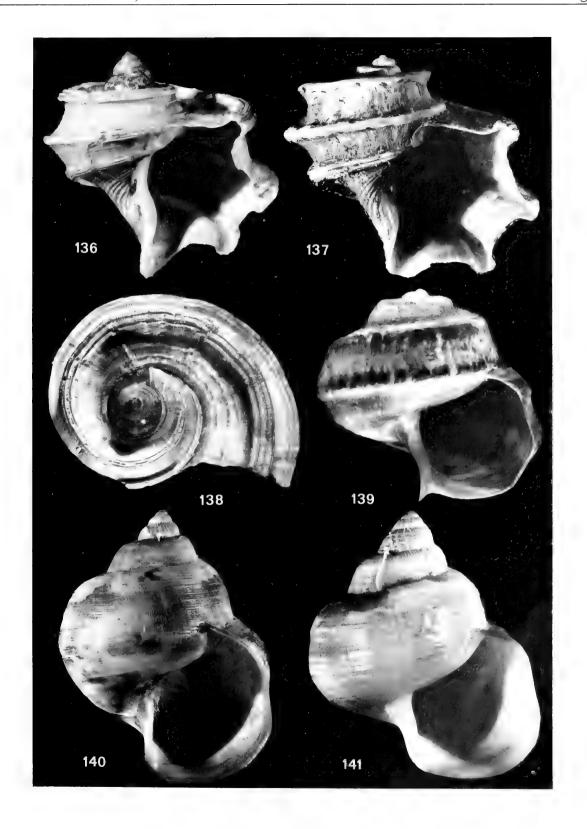
Figures 137 and 138. *A. orientalis,* holotype, diameter 15 mm.
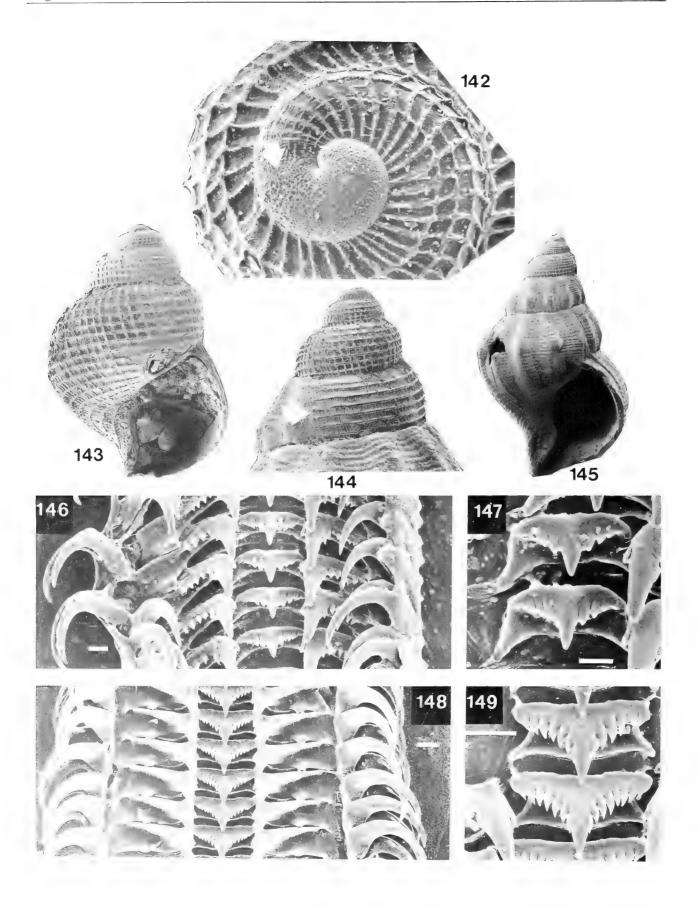
Figure 139. *A. schepmani,* holotype, diameter 5.9 mm.

Figure 140. *A. flexibilis,* holotype, diameter 18.0 mm.

Figure 141. *A. flexibilis* (S of Zanzibar, USNM), height 15 mm.

planktotrophic development. We also figure the apical whorls of *Ficus subintermedia,* which has a multispiral protoconch and may indicate planktotrophic larval development.

Thalassocyon Barnard, 1960

Thalassocyon BARNARD, 1960:440.

Type species: By original designation, *Thalassocyon bonus* Barnard, 1960, recent, deep water off South Africa.

Remarks: The Ficidae contains mainly shallow-water species, but *Thalassocyon* Barnard, 1960, of which two nominal species have been described, is only known from depths below 1000 m. BEU (1969) transferred the genus from Cymatiidae where Barnard described it to the Ficidae because of shell and radular morphology.

Recently we became aware that J. Knudsen (unpublished) had started, long ago, a treatment of the specimens of *Thalassocyon* taken by the Galathea Expedition in the Kermadec Trench (BEU, 1969), with the intention to describe their morphologies and to synonymize *T. tui* Dell, 1967, with *T. bonus.* This work had never been finished and when he learned of our intentions to do the same, he made his notes and material available to us.

One half-grown shell of *Thalassocyon* (NMNZ M 35293), from off East Cape, New Zealand, 1000 m, with a badly corroded apex, had brownish fragments remaining from the larval shell. The species possibly has planktotrophic larval development.

Anatomy of *Thalassocyon*

The foot is small, with wrinkled sides and a distinct propodium. It lacks a posterior pedal gland and the drawn out anterior corners that are present in *Ficus*. The operculum is small, black, and circular, with a lateral, corroded nucleus (similar to that of *Distorsio*) and does not fill the aperture. The head is large and broad compared with *Ficus* and does not have a long slender neck. The tentacles are short and conical and lack eyes.

The pallial cavity is large and spacious, with a simple, muscular margin that does not cover the outside of the shell (which is indicated by the thick, bristly periostracum). The inhalant siphon is thick and muscular, strongly con-

tracted. An exhalant siphon is indicated by a triangular lobe at the right extremity of the pallial edge.

The male has a long, slender, simple, finger-shaped penis, to which the sperm is transported via a simple, narrow, open furrow that crosses over to the side of the pallial cavity and backwards. The rectum is simple and opens far back in the pallial roof; in the female it runs between the pallial oviduct and the pallial skirt. The rectum of three specimens contained numerous, large fecal pellets, neatly aligned and connected by mucus strings. Identifiable contents were sand, numerous pieces of cuticle, and large quantities of broken polychaete bristles, somewhat similar to the large bristles of the families Aphroditidae and Amphinomidae.

The gill occupies almost the whole distance from the bottom to the opening of the pallial cavity and consists of about 60 triangular leaflets, which are 1.6 mm wide and 2.0 mm high in the central part of the gill. The osphradium is regularly bipectinate with about 40 pairs of high leaflets.

The proboscis is simple and can probably be extended to a length approaching the length of the shell (partly everted in one specimen). In the retracted state it occupies the anterior, dorsal $\frac{1}{6}$ of the volume of the cephalo-pedal haemocoel. The buccal mass is small and slender, with a pair of jaws similar to those of *Ficus*. The anterior oesophagus is slender and fused with the thick-walled salivary ducts, which pass through the nerve ring on their way to the two large, simple salivary glands that lie in the anterior part of the cephalo-pedal haemocoel. The salivary glands abut the cerebral ganglia and are pushed forwards by the huge oesophageal gland, which fills $\frac{5}{6}$ of the cavity. The gland is solid and consists of numerous thick, spongy, transversal folds.

Radula. See Figures 1 and 2. The size is remarkably only $\frac{1}{4}$–$\frac{1}{5}$ that of a specimen of *Ficus subintermedia* of the same size.

The nervous system was not examined.

Thalassocyon bonus Barnard, 1960

(Figures 1, 2, 132–135)

Thalassocyon bonus BARNARD, 1960:440.
Thalassocyon tui DELL, 1967:309. (New synonym.)

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Explanation of Figures 142 to 149

Kaiparanura, shells; *Ficus* and *Distorsio*, radulae.
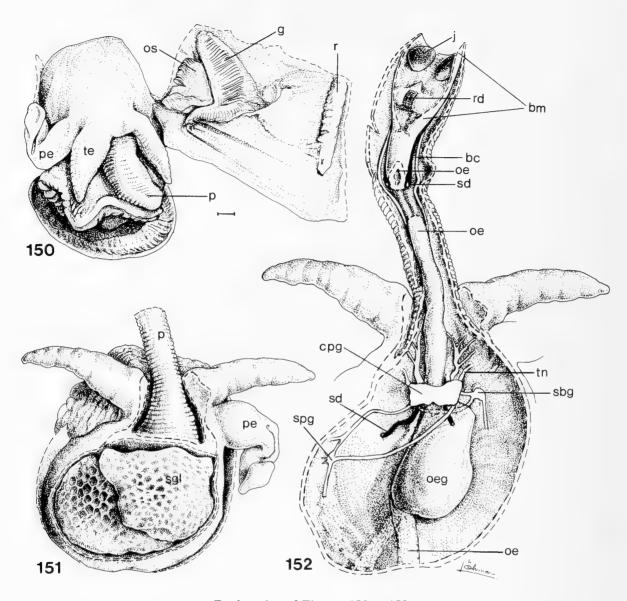
Figures 142 and 143. *Kaiparanura spiralis,* larval shell (NMNZ), diameter of protoconch I, 225 µm (border to teleoconch indicated by arrow); height of larval shell (Figure 143), 2.75 mm.

Figures 144 and 145. *K. spiralis,* complete shell (Figure 145) and apex (Figure 144) (NZGS). The white arrow indicates border

between larval shell and teleoconch. Height of larval shell (Figure 144), 2.0 mm; height of shell (Figure 145), 7.5 mm.

Figures 146 and 147. *Distorsio clathrata* (SMNH), radula. Scale lines 10 µm.

Figures 148 and 149. *Ficus subintermedia* (New Caledonia, MNHN), radula. Scale lines 50 µm.

Explanation of Figures 150 to 152

Anatomy of *Oocorys sulcata* (off Portugal, MNHN). Scale line 1 mm.

Figure 150. Head-foot, pallial skirt. External features.

Figure 151. Body cavity opened to show salivary glands.

Figure 152. Body cavity and proboscis opened, salivary glands removed.
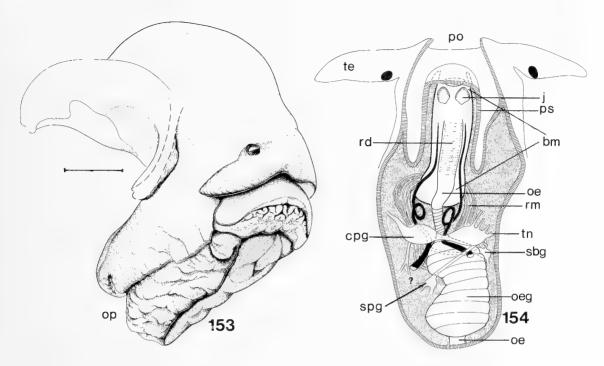
Key: bc, buccal cavity; bm, buccal mass; cpg, cerebro-pleural ganglion; g, gill; j, jaw; oe, oesophagus; oeg, oesophageal gland; os, osphradium; p, proboscis; pe, penis; r, rectum; rd, radula; sbg, suboesophageal ganglion; sd, salivary duct (marked black); sgl, salivary gland; spg, supraoesophageal ganglion; tn, tentacle nerve.

Type material: *Thalassocyon bonus*, holotype SAM A 9714; *T. tui*, holotype NMNZ M 21299.

Type localities: *Thalassocyon bonus*, 33°26'S, 16°33'E, 2280–2400 m, off western South Africa; *T. tui*, 30°11'S, 179°52'W, 1152–1205 m, W of Kermadec Islands.

Material examined: The type material; off South Africa,

33°49'S, 16°30'E, 2760 m, paratype, SAM A 9756; 34°37'S, 17°03'E, 2900–2980 m, paratype, SAM A 9759; 33°50'S, 16°30'E, 2720–2945 m, paratype, SAM A 9810; New Zealand, NE of Chatham Id., 42°56.3'S, 175°05'W, 1004–1011 m, 1 shell, NMNZ 75253; Lord Howe Rise, NZOI sta. P120, 35°45.7'S, 165°04.1'E, 950 m, 1 shell, NZOI; 30°11.5'S, 179°52'W, 965–975 m, holotype, NMNZ M 21299; NZOI sta. J41, 36°50'S, 170°13'E, 2060 m, 1 spec-

Explanation of Figures 153 and 154

Anatomy of *Pisanianura breviaxe*.

Figure 153. Head-foot, pallial skirt removed. Scale line 2 mm.

Figure 154. Schematic plan over body cavity, salivary glands removed.

Key: bm, buccal mass; cpg, cerebro-pleural ganglion; j, jaw; oe, oesophagus; oeg, oesophageal gland; po, proboscis opening; ps, proboscis skirt; rd, radula (seen by transparency); rm, retractor muscles; sbg, suboesophageal ganglion; spg, supraoesophageal ganglion; te, tentacle; tn, tentacle nerve; ?, zygoneury not verified.

imen, NZOI; NZOI sta. P940, 41°22.7′S, 166°44.4′E, 2092–2154 m, 1 shell, 1 specimen, NZOI; 36°40.1′S, 172°44.7′E, 1622–1634 m, 1 specimen, NMNZ M 74630; NZOI sta. P941, 41°15.2′S, 167°07.2′E, 1457–1463 m, 1 specimen, NZOI; off East Cape, 37°30′S, 179°22′E, 1140–1215 m, 1 young shell, diam. 12.9 mm, NMNZ 35293; S of Amsterdam Id., R/V *Marion Dufresne* cruise MD50 sta. DC167, 38°24′S, 77°29′E, 1430–1600 m, 1 worn shell, MNHN; off Queensland, ca. 2000 m, 1 specimen, AMS (uncatalogued); Galathea Expedition sta. 665, Kermadec Trench, 36°38′S, 178°21′E, 2470 m, 2 specimens, ZMC; Galathea Expedition sta. 668, Kermadec Trench, 36°23′S, 177°41′E, 2640 m, 4 specimens, 1 shell, ZMC.

Distribution: From South Africa, west to the Kermadec Islands, abyssal.

Remarks: During our search for larval shells of *Thalassocyon* we examined all specimens of the genus in AMS, NMNZ, SAM, and MNHN. When the two nominal species were described they were known only from a very few specimens from South Africa and New Zealand. The richer material now available, including specimens from Queensland (*Thalassocyon* was also recently recorded from off New South Wales, 570–950 m, by COLMAN, 1987) and Amsterdam Island, indicates that the specimens from South Africa and New Zealand can hardly be distinguished, al-

though specimens from South Africa usually have a taller spire than those from New Zealand. Specimens from Amsterdam Island, which are geographically intermediate, however, are intermediate in this character and we suppose there is a cline in the height of the spire (Figures 132–135).
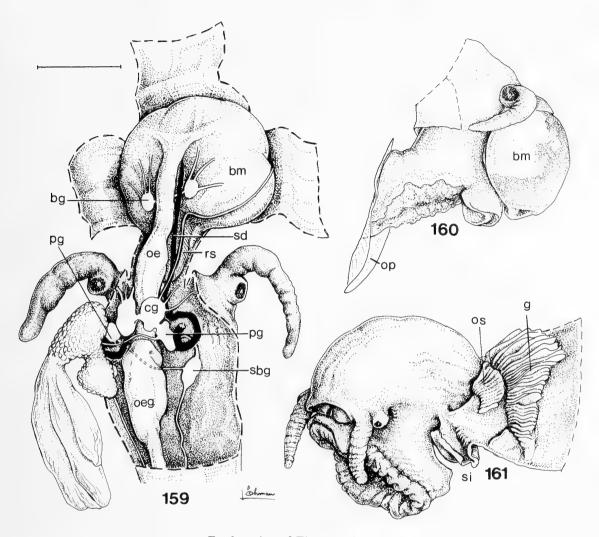
Family TONNIDAE Suter, 1913

(Figures 9–14, 49, 61, 62, 73–79)

The Tonnidae is mainly restricted to shallow water, above 100 m. We figure radulae and jaws, as well as the shell, operculum, and the radula of a larva for comparison with other families. The only genus that occurs in deep water is *Eudolium* Dall, 1889. The type species, *E. crosseanum*, was discussed and several shells figured by PIANI (1977). The species of the genus were reviewed by CERNOHORSKY (1976). We illustrate a young specimen from the Azores with an intact larval shell (Figures 78, 79) and the radula (Figure 11).

The larva of *Tonna* has been figured and described several times (*e.g.*, MACDONALD, 1855; FISCHER, 1863; DAWYDOFF, 1940; LAURSEN, 1981).

The competent larva has an uncalcified shell (Figures 73, 74) of about 5 mm in diameter. Immediately after

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158

Explanation of Figures 159 to 161

Anatomy of **Laubierina peregrinator**.

Figure 159. Dissection of body cavity.

Figure 160. Head-foot, right side, buccal mass partly everted, pallial skirt removed.

Figure 161. Head-foot, right side.

Key: bg, buccal ganglion; bm, buccal mass; cg, cerebral ganglion; g, gill; oe, oesophagus; oeg, oesophageal gland; op, operculum; os, osphradium; pg, pleural ganglion; rs, radular sac; sbg, suboesophageal ganglion; sd, salivary duct; si, siphon.

Explanation of Figures 155 to 158

Anatomy of *Akibumia* sp.

Figures 155 and 156. *A schepmani,* head-foot (Figure 155) and organization of body cavity; salivary glands and most of oesophagus removed (Figure 156).

Figures 157 and 158. *A orientalis,* organization of body cavity; salivary glands removed (Figure 157) and head-foot without pallial skirt (Figure 158).

Key: bm, buccal mass; bg, buccal ganglion; cg, cerebral ganglion; cpc, cerebro-pedal connective; oe, oesophagus; oeg, oesophageal gland; pg, pleural ganglion; ppc, pleuro-pedal connective; ps, proboscis sheath; rm, retractor muscles; rs, radular sac; sbg, suboesophageal ganglion; sd, salivary duct (marked black); spg, supraoesophageal ganglion; te, tentacle; tn, tentacle nerve; 1, nerve to mouth; 2, nerve to lips and proboscis sheath; 3, nerve to lips and buccal mass; ?, zygoneury not verified.
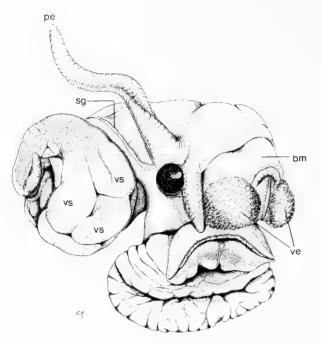
Figure 162

Recently metamorphosed young of **Laubierina** sp. (Mozambique Channel).

Key: bm, partly everted buccal mass; pe, penis; sg, seminal groove; ve, remains of velum; vs, vesicula seminalis.

settlement the animal starts to fill it internally with calcium carbonate. When the animal gets older the larval shell finally becomes totally solid. If then the old periostracum starts to decay (which evidently does not always happen), only the internal mould remains (Figure 76). The same development of the larval shell occurs in *Eudolium*. The internal mould shown in Figure 76 was obtained from the shell in Figure 75 by dissolving the periostracum in bleach.

The competent veliger larva of *Tonna* has a radula similar to that of the adult (Figures 9, 10).

Family CASSIDAE Latreille, 1825

(Figures 15–24, 50, 51, 63–66,
115–120, 150–152)

Since ABBOTT's (1968) and BEU's (1976, 1981) treatments of members and classification of the family, *Morum* Röding, 1798, has been shown to belong to the Harpidae (HUGHES, 1986b); subgenera and synonyms of *Morum* are reviewed by BEU (1976).

Several radulae and opercula of *Cassis* Scopoli, 1777, have been figured by ABBOTT (1968), BANDEL (1984), BAYER (1971), and TROSCHEL (1863), and we illustrate those of *Galeodea echinophora* (Figures 17, 18, 22), *Semicassis granulatum* (Figures 19, 20), and *Semicassis saburon* (Figure 21) for comparison.

The cassids have a smooth, round larval shell of several whorls, calcified also in the veliger larva, that was described in general for several species by ABBOTT (1968) and in detail by LAURSEN (1981) for *Semicassis granulatum* and *Cypraecassis testiculus* (Figures 115–117). The operculum of the Phaliinae (*Semicassis* Mörch, 1852, *Phalium* Link, 1807, *Casmaria* H. & A. Adams, 1853, and *Echinophoria* Sacco, 1890, among others) is of an unusual type in being very slender, with a lateral nucleus at half the length, and is sometimes equipped with strong radial ribs (Figure 65). This has been described for several species by ABBOTT (1968). In *Semicassis granulatum* the larval operculum (Figures 63, 64) can be seen also in adult specimens. In the deep-water genus *Oocorys,* the operculum is simply paucispiral, which is one of the characters that induced FISCHER (1883) to erect the genus.

The larva of *Oocorys* is not known. DALL (1889) and TURNER (1948) reported that the larval shell consists of 2–2.5 whorls that are smooth or sculptured in the same way as the teleoconch. QUINN (1980) described that of *Oocorys caribbea* Clench & Aguayo, 1939, as multispiral and reticulated. We have seen some remains of a reticulated larval shell on specimens of *Oocorys umbilicata* and *O. bartschi* (Figures 118, 119).

Competent cassid larvae have a radula similar to that of adults, but with weaker and more membranaceous teeth (Figure 23). The larvae of *Semicassis granulatum* and *Cypraecassis testiculus* have an indistinctly bipectinate osphradium, with those leaflets facing away from the gill being much smaller.
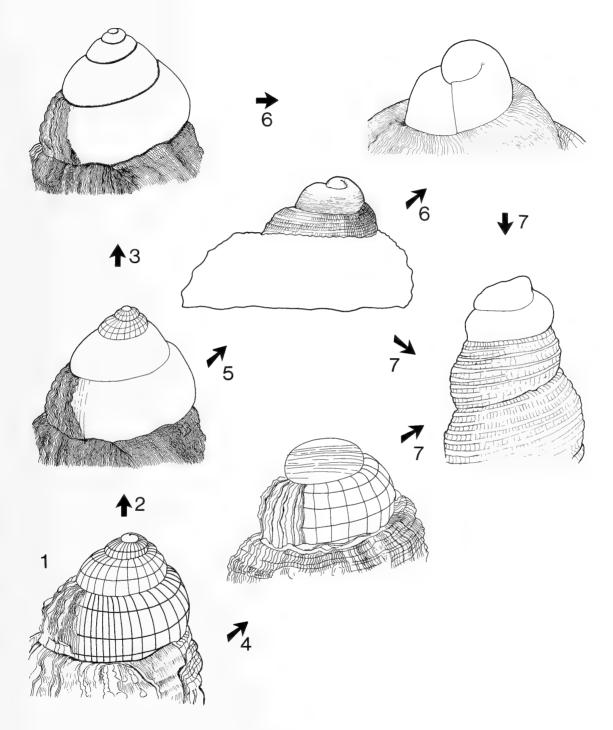
Position of Oocorythidae Fischer, 1885

The "family" Oocorythidae has usually been regarded as a subfamily of the Tonnidae (THIELE, 1929; WENZ, 1941; BOSS, 1982). DALL (1909) concluded that the Oocorythidae could not be distinguished from the Cassidae, a conclusion disputed by QUINN (1980). Quinn discussed the systematic position and status of the family and concluded that it was distinct from the Tonnidae and contained the genera *Oocorys* Fischer, 1883, *Hadroocorys* Quinn, 1984, *Dalium* Dall, 1889, *Galeoocorys* Kuroda & Habe, 1957, and perhaps also *Galeodea* Link, 1807. PONDER (1984) agreed with BEU (1981) who placed Oocorythidae as a

→

Figure 163

Principles and possible pathways of the evolution of the larval shell of the Tonnoidea.

1. This is considered the ancestral type of planktotrophic larval shell.

2. Changes in the protoconch II primarily affect the later part of the shell, and usually consist of loss of sculpture.

3. Loss of calcification can also happen independently of stage in development, but because it seems to be an adaptation to long-lasting planktotrophic life, it normally happens only in such species.

4–6. Loss of planktotrophy can take place from any stage in the evolution of the planktotrophic larval shell. This leads to a paucispiral larval shell, where the original sculpture may remain or finally may be lost, as in Figure 6.

7. Calcification of the aperture before the initial whorl (as in *Sassia* [*Austrosassia*] spp., see BEU, 1988a) is still another modification of the intracapsular development (well known from the Buccinidae).

This scheme is not supposed to show the actual evolution within the superfamily, but only to give examples of the direction of the evolution.

subfamily of Tonnidae, but placed *Galeodea maccamleyi* Ponder, 1984 in the Cassinae. (Ponder's description of that species contains good anatomical information and excellent figures of the radula, jaws, and operculum.)

We find the placement of the Oocorythidae as a subfamily of the Tonnidae untenable because of the differences in the radula (Figures 9–14 vs. 15–24), jaws (Figures 49 vs. 50 and 51) and operculum (Figures 61 and 62 vs. 63–66). On the other hand, we can see no strong arguments against the association of Oocorythidae with the Cassidae. The radulae are quite similar (Figures 15, 16, and 24, and pointed out by BANDEL, 1984). Also, the soft parts are similar as far as we can see from the few descriptions of cassid anatomy that have been published (*e.g.,* QUOY & GAIMARD, 1835; PANCERI, 1869; REYNELL, 1905, 1906; WEBER, 1927; HUGHES & HUGHES, 1981), from QUINN's (1980) description and our own dissections of *Oocorys sulcata* (Figures 150–152), and from HALLER's (1893) description of *Galeodea echinophora*. Finally, the shells form a continuous series of increasing complexity of the incremental scars and siphonal canal (*Oocorys-Galeodea-Cypraecassis-Cassis*). The only difference from the cassids pointed out by QUINN (1980) is that the cassids are supposed to have the tip of the inner marginal tooth equipped with denticles (sometimes also present on the outer marginal, *cf.* ABBOTT [1968] and BANDEL [1984]). These denticles were said to be absent in *Oocorys*. We have, however, found such denticles in *Oocorys sulcata* and *Galeodea echinophora* (Figures 22, 24).

We therefore consider that the Oocorythidae should be included in the Cassidae (as does A. Beu, pers. comm., who also suggests that they should be classified in the Cassinae). Whether it should be kept as a distinct subfamily or not, we cannot say.

Family BURSIDAE Thiele, 1925

(Figures 5–8, 58–60, 110–114)

BEU (1981) gave a detailed description of the Bursidae and described the soft parts for several species, in addition to summarizing earlier knowledge on the family. LAURSEN (1981) described the larva of some western Atlantic *Bursa* Röding, 1798, and RISBEC (1955) described the gross morphology of *Bursa* from New Caledonia. BANDEL (1984) questioned the validity of the Bursidae as a family, but this was based only on the comparison of radulae with those of the Cymatiidae.

We find the Bursidae a well-defined unit, characterized by several independent characters (*i.e.,* posterior canal, reduced jaws, 3 accessory salivary glands [Beu, pers. comm.], globular, calcified larval shell, and similar teleoconchs) and support Beu's view. We figure the larval shell, operculum, and radula (which shows a remarkable similarity to the Tonnidae) for comparison (Figures 5–8, 58–60, 110–114) with other Tonnoidea. We examined several larvae but did not succeed in finding a radula.

DE FOLIN (1884:212) described the larva of an unidentified *Bursa* from southwestern Europe or western Africa as *Talisman parfaiti* (types examined in MNHN). The generic name *Talisman* de Folin, 1884, will not interfere with any of the generic names normally in use for bursids from that area because those all are older.

Family PERSONIDAE Gray, 1854

(Figures 84, 121, 122, 146, 147)

The Personidae is characterized by the central radular tooth with distinct, down-curved corners, a periostracum as in the Ranellinae, and a long proboscis that in the retracted state is coiled. The shell has (in Recent species) a strongly developed parietal shield, a small aperture, and characteristic columellar ridges and denticles.

The larva of *Distorsio* Röding, 1798, was described by LAURSEN (1981) and from the similarity of his figure and the original figure of *Calcarella* Souleyet, 1850, we conclude that they refer to closely related species. We also conclude that one of the "giant veligers" described by DAWYDOFF (1940:fig. 2) belongs to the same group, and that the larva described by SIMROTH (1911) under the name *Calcarella spinosa* Souleyet is closely related. BEU (1987:figs. 133, 137 139) figured the larval shell of a young specimen with parts of the strongly developed periostracal fringes remaining. We figure a recently metamorphosed larva with traces of post-larval growth (Figure 84) and the apex of *Distorsio* sp. (Figure 122). The larval shell is similar to that of *Bursa* spp., but differs by having smooth initial whorls. *Distorsionella lewisi* Beu, 1978a, from about 600 m depth, north of New Zealand, has a reticulated larval shell, but the corresponding larva is not known. The protoconch is figured here (Figure 121). This larva presents a problem in the determination of developmental type. The sculpture on the protoconch certainly is the type found in species with planktotrophic development, but at the same time it has fewer whorls than what is normal in those, and we believe that it does not have planktotrophic development.

DISCUSSION

The Use of Larval Shells in Classification

Two contrary views on the phylogenetic significance of the different types of protoconchs have been expressed for several decades. One point of view was expressed by DALL (1924): "In common with most students of the Mollusca for some years I have regarded the nucleus characters as more or less indicative of genetic affinity, but recently having had to work over large numbers of deep water species, especially toxoglossate forms, and to utilize Hedley's fine monograph of the Australian Turridae, I have found this view to involve so many apparently preposterous combinations of unlike things and separation of similar things, that I have come to the conclusion that this view

cannot be maintained." And further: "When two marine forms of similar anatomical structure exhibit different nuclei, I conclude that the adaptive modification is not of serious value in classification, and in most cases should not be considered as of more than sectional or subgeneric importance. The parallel occurrence of similar nuclei in widely different groups of families is obviously no indication of genetic affinity."

Exactly the opposite view was held by FINLAY (1931) who emphasized that the protoconch was a good character for classifying Tonnoidea: "I think the only satisfactory basis for the classification of the Cymatiidae is the protoconch, and would reject a species from any of the shell groups if it does not agree with the other members in apex." And further: "After a number of years careful examination of gastropod apices, I am fully satisfied, in spite of what several authors have written, that the protoconch is one of the most valuable criteria for systematic classification. Not only have I never found it to vary from type in a homogeneous genus, but I have also found it so generally constant that in my opinion considerable importance must be placed on it in determining lineage relationships. To the palaeontologist it is as important as the radula is to the malacologist, and should be given just as much consideration."

After scientists had noticed the occurrence of very different types of larval shells within a well-defined genus, the larval shell has obtained a bad reputation as a systematic character among many malacologists, while others have uncritically used this to separate genera. To understand these discrepancies it is necessary to consider the evolutionary background.

Planktotrophic larval development is considered to be the ancestral mode of development in marine invertebrates in general (STRATHMANN, 1978, 1985), and in marine gastropods in particular (JABLONSKI & LUTZ, 1983). Nonplanktotrophy is a derived condition that has appeared, obviously independently, in different families and genera. Each time such a change takes place, it affects only a single species or population. This species may then give rise to a new lineage, characterized by non-planktotrophic development, or may become extinct. Such changes have been documented by paleontologists. A reversal, from nonplanktotrophy to planktotrophy, has not been documented and seems less likely, at least if the larval development has been modified so much that the larva has lost the ability to swim or feed on plankton.

When a species changes from planktotrophic to lecithotrophic development, the larval shell, too, is affected, and must therefore be regarded as a new, acquired character.

With this background knowledge, we assume that the two views on the systematic value of the larval shell are the result of lack of discrimination between larval shells of different developmental types, and we can see (as did MARSHALL, 1978) no reason why species with different types of development necessarily have to be classified in different subgenera or genera, as often has been emphasized. (BOUCHET [1989] has reviewed a number of cases of closely related prosobranch species that differ almost only by having plankto- and lecithotrophy, respectively, and correspondingly different types of larval shells.)

We also assume that as long as larval shells of planktotrophic larvae are compared, they are good indicators of relationship and have the same taxonomic value as teleoconchs. Among those sharing the view of FINLAY (1931) on the other hand, the protoconch has been overestimated in value, and used in the wrong way, by comparisons made among protoconchs with different biological origins.

Larval Development of Tonnoidea

Detailed descriptions of the spawn (AMIO, 1963; LAMY, 1928; PENCHASZADEH, 1981; PETIT & RISBEC, 1929; RISBEC, 1931, 1936; THORSON, 1940) and early development of tonnoid larvae exist, covering the time until hatching (ANDERSON, 1959, 1966; BANDEL, 1975; D'ASARO, 1969; GOHAR & EISAWY, 1967; HUGHES, 1986a; LAXTON, 1969; PHILPOTT, 1925). The development of the later larva, however, has attracted less attention and little detailed information exists; but as in most caenogastropod taxa, planktotrophy and lecithotrophy are reflected in the morphology of the larval shell, in accordance with THORSON's (1950) "apex theory" and other references cited by ROBERTSON (1976).

Most species that have been described in detail leave the egg capsule as planktonic veliger larvae with a shell of a diameter of up to 0.4 mm and consisting of less than one whorl, which constitutes protoconch I. (Reports on presumed adelphophagy in *Tonna* [PENCHASZADEH, 1981] discussed by HOAGLAND & ROBERTSON [1988] and BOUCHET [1989] need confirmation, but do not change our discussions.)

The first discontinuity in the shell surface indicates the moment of hatching and separates protoconch I from protoconch II, which is formed during the time the larva feeds on phytoplankton. Protoconch II consists of 2.5–4 whorls, and its diameter is 1–5 mm. After metamorphosis, the young benthic snail secretes the teleoconch, which is separated from protoconch II by a second discontinuity. The two discontinuities, reflecting hatching and metamorphosis, can be observed on the apical parts of well-preserved Recent and fossil shells (Figures 73–79, 87, 88, 101–103, 106–109). Without consideration of the mode of the development, a protoconch is always present and statements indicating the absence of protoconch in some tonnoid taxa (BEU, 1988a:1) are erroneous, although in some species it is not clearly demarcated, or in certain species with lecithotrophic development it may be only partly calcified or in other ways changed because of the specific ontogeny.

Of the tonnoids with detailed information on the mode of development, *Galeodea echinophora* hatches as a crawling juvenile; its larval shell has a diameter of 1.1–1.6 mm

(HUGHES, 1986a) and a single discontinuity is present on the apical part of the shell, demarcating the protoconch from the teleoconch (Figure 120).

BEU (1988a) described the development of *Sassia (Austrotriton) subdistorta* (Lamarck, 1822), which never forms a normal protoconch I. This species has lecithotrophic development, and the initial whorl is not calcified until late and has the appearance of being incomplete or broken.

Occurrence of non-planktotrophic development is also known, from indirect (protoconch) evidence, in other Cassidae and Ranellidae (examples: species of *Sassia,* see KESTEVEN, 1902:figs. 1–6, BEU, 1987:figs. 127, 130, and this paper, Figure 91; *Sassia [Cymatiella],* see BEU, 1988a: figs. 18–21; *Eocymatium pyraster* (Lamarck, 1803), see BEU, 1988b:text-fig. 1G).

LAURSEN (1981) described and figured a larva as "unidentified larva A." Judging from his figures and description, and considering the genera known or presumed to occur in the area where this larva was taken, this may be the larva of a species of *Pisanianura, Oocorys,* or possibly *Gyrineum* Link, 1807. The shape and the sculpture agree and the size range given by Laursen (2.5–3.5 mm) covers all our measurements from preserved apices. His drawings were prepared from specimens close to metamorphosis as is indicated by the ribs being more crowded towards the outer lip. According to Laursen, as many as 2782 specimens were caught between 5° and 35°N in the Atlantic and it was said to be the fifth most common species in his material of 38,000 prosobranch larvae. We have tried to examine Laursen's figured specimens for direct comparison, but it proved impossible to find them in the Zoological Museum in Copenhagen, where this material is kept. Several samples labelled "A" contained mixtures of typical *Cymatium* larvae (*e.g.,* our Figure 98).

Systematical Implications of the Larval Shell Morphology in Tonnoidea

The first result of our discussions above is that we agree with SMITH (1945), who advocated *Ficus* to be a monophyletic genus despite the occurrence of multispiral and paucispiral larval shells in the genus. We do, however, exclude the Ficidae from further comparisons with other Tonnoidea because of the very different larval shell.

Our view on the controversy about larval shells does not imply that genera or subgenera comprising only species with non-planktotrophic development are necessarily polyphyletic. For instance, *Sassia (Austrotriton)* is defined by BEU (1988a, b) as a subgenus containing "fossil and living species with caricelloid apices (. . .), reflecting direct development." This shared apical morphology (and mode of development) may be the result of convergence (with *Austrotriton* being polyphyletic) or may be derived from a common ancestor (with *Austrotriton* being monophyletic). Evidence for this is to be looked for in the other shell characters and history of the group, as BEU (1988a) also

did after, we think, overemphasizing the importance of the protoconch. Similarly, we find the erection of *Eocymatium* Beu, 1988b, for a species with a paucispiral protoconch indicating lecithotrophic larval development not justified on the basis of that character alone. Again here we do not mean that *Eocymatium* is not a valid genus, but certainly its mode of larval development by itself does not justify erection of a new genus and Beu (pers. comm.) has emphasized that these two genera also are based on other characters.

The planktotrophic larval shell of tonnoids exhibits great variation between different families, when genera such as **Laubierina,** *Cymatium,* and *Semicassis* are compared. On the other hand, one shell type is represented in several families and subfamilies—a globular shell with a distinct sculpture of thin axial and spiral cords, sharply set off from a smooth surface and intersecting at right angles. *Sassia remensa* (Figure 90) and *S. raulini* (Figure 94) can be taken as examples of this.

A similar sculpture is known from the Cypraeoidea (*e.g.,* RICHTER & THORSON, 1975), the Cancellariidae (Beu, pers. comm.), the Trichotropidae (Warén, unpublished), and the Elachisinidae (Warén, unpublished). In the Trichotropidae, however, this sculpture appears only at the last part of the larval shell and, in the other groups, the ribs are much broader and constitute most of the surface, so that there are no large, smooth interspaces. Therefore we consider the similarity of larval tonnoid shells to those of the other families to be due to convergence.

Reticulated larval shells, similar to those of *Sassia,* occur in the following families and subfamilies: Personidae, **Laubierinidae,** "Oocorythinae," Neptunellinae, and **Pisanianurinae.**

The groups that only have other types of planktotrophic larval shell are the Bursidae, some Cassidae, the Tonnidae, *Cymatium, Charonia,* and the Ranellinae. In the last four cases all species have a chitinous larval shell that has been interpreted as an adaptation to long planktonic life (PECHENIK *et al.,* 1984). Nevertheless, it shows the typical sculpture on the first part of protoconch II (Figures 77, 79, 103, 104).

In the Personidae we are not sure about the interpretation of the larval shell of *Distorsionella* (Figure 121), but it shows the typical reticulate sculpture.

In the Bursidae and Cassidae (Figures 110–117) only the first part of protoconch II has the typical reticulate sculpture, but still it is identical to that in *Sassia.*

In all of these taxa (except **Laubierinidae** and **Pisanianurinae**), there exist also larval shells without or with only very weak sculpture. This we consider a modification by loss of the net-sculpture, in the same way as it is lost on the later part of protoconch II in *Bursa* (Figure 110). There is no case in which an obviously different type of sculpture has evolved.

It is obvious and worth noting that the reticulate sculpture on planktotrophic larvae is better developed in the

deep-sea representatives of the different families. It is more pronounced in *Eudolium* (Figures 78, 79) than in *Tonna* (Figures 76, 77); it is present in *Distorsionella* (BEU, 1978a: fig. 5; this paper, Figure 121), a genus only known from moderately deep water, but absent in *Distorsio* (Figure 122), which is restricted to shallow water. It is strongly developed in many species of *Sassia* (Figures 90, 92), a genus of Ranellidae that had its distributional maximum in the early and mid-Tertiary, and is now restricted to deep water. It is also present in *Oocorys* (Figures 118, 119), but not in the shallow-water cassids. It is also the only type of larval shell known in the **Laubierinidae** and **Pisanianurinae**, both deep-water groups.

We therefore assume that this reticulate sculpture reflects the original condition in the Tonnoidea and that it has subsequently been modified in the more-advanced shallow-water and/or Recent representatives of the superfamily.

This conclusion has been summarized in Figure 163.

It is also obvious, from the discussions above, that the larvae of the Tonnoidea can be determined with good accuracy, at least to subfamily or genus, from existing knowledge. For specific determinations one still must rely on direct comparison of young specimens with preserved larval shells.

We have therefore compiled a key to the planktonic larvae of Tonnoidea.

Tentative Key to the Planktonic Larvae of Tonnoidea

A. Shell calcified, completely covered by reticulate
   sculpture .... **Laubierinidae**
                                     Pisanianurinae
                       Neptunellinae (some *Sassia*)
                              Cassidae (*Oocorys*)
                        Personidae (*Distorsionella*)
                             Ranellinae, *Gyrineum* sp.
A. Shell mostly smooth, sometimes with reticulate
   sculpture on apical whorls .... B
B. Shell calcified C
B. Shell not calcified .... E
C. Shell completely smooth .... D
C. Apical whorls with reticulate sculpture ... Bursidae
D. Operculum with internal ridge, radular teeth
   membranaceous .... Cassidae (excl. *Oocorys*)
D. Operculum without internal ridges, radular teeth
   normal .... Neptunellinae (some *Sassia*)
E. Shell with tall spire .... Neptunellinae
E. Shell globular .... F
F. Shell smooth .... Tonnidae
F. Shell with strongly developed periostracal fringes
   .... Personidae (excl. *Distorsionella*)
                                        Ranellinae

Remarks: The family Ficidae is not included in the key because of incomplete knowledge. See remarks under that

family. A complete larval shell of Oocorythinae has not been examined, but we know it to be reticulated (Figures 118, 119).

ACKNOWLEDGMENTS

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APPENDIX: LIST OF SPECIMENS FIGURED

FICIDAE

Thalassocyon bonus, NZOI sta. P941, Tasman Basin, 41°15.2′S, 167°07.2′E, 1452-1463 m (NZOI). Figures 1, 2.

Thalassocyon bonus, off East Cape, New Zealand, 37°30′S, 179°22′E, 1128-1200 m (NMNZ M 35293). Figure 133.

Thalassocyon bonus, NE of Chatham Id., New Zealand, 42°56′S, 175°05′W, 1004-1011 m (NMNZ M 75253). Figure 134.

Thalassocyon bonus, S of Amsterdam Id., MD50 sta. DC167, 38°24′S, 77°29′E, 1430-1600 m (MNHN). Figure 135.

Thalassocyon bonus, holotype (SAM A 9714). Figure 132.

Ficus communis Röding, 1798, Florida (SMNH). Figure 80.

Ficus sp., Seychelles, Reves 2 sta. 42, 04°31′S, 56°09′E, 52 m (MNHN). Figures 3, 4.

Ficus conditus (Brongniart, 1823), St. Paul les Dax, SW France, Burdigalien, lower Miocene, P. Lozouet coll. (MNHN). Figure 81.

Ficus sp., Philippines, Musorstom 3 sta. CP100, 14°00′N, 120°18′E, 189-199 m (MNHN). Figure 82.

Ficus subintermedia (d'Orbigny, 1852), New Caledonia, Musorstom 4 sta. CP148, 19°23′S, 163°32′E, 58 m (MNHN). Figures 148, 149.

BURSIDAE

Bufonaria marginata (Gmelin, 1791), Canaries, Gran Canaria, off La Luz, 100 m, coralline algae (SMNH 3271). Figures 7, 8.

Bufonaria marginata, off Mauretania, 18°54′N, 16°32′W, 60 m (MNHN). Figures 113, 114.

Bursa sp., Gilbert Id., Aranuka (SMNH 3853). Figures 5, 6, 59, 60.

Bursa sp., larva, Demeraby sta. DS02, 08°10′N, 49°05′W, 4430 m (MNHN). Figures 58, 110-112.

TONNIDAE

Tonna sp., larva, off SE South Africa, 33°34′S, 27°41′E, surface plankton, 10 Oct. 1902 (SMNH 2717). Figures 9, 10, 61, 62, 73, 74.

Tonna galea (L., 1758), Malta (SMNH). Figure 75.

Tonna galea, Macahé, Isla Santa Anna, off Rio de Janeiro, Brasil (SMNH). Figures 76, 77.

Tonna sp., Tamatave, Madagascar, young specimen (SMNH 2676). Figure 12.

Tonna allium (Dillwyn, 1817), Sumatra, Priaman (SMNH 474). Figures 13, 14, 49.

Eudolium crosseanum (Monterosato, 1869), Biacores sta. 161, the Azores, 37°40'N, 25°51'W, 590 m, young specimen, height 26.1 mm (MNHN). Figures 11, 78, 79.

CASSIDAE

Oocorys sulcata (Fischer, 1883), off S Portugal, Noratlante sta. B12, 36°22'N, 08°43'W, 2873 m (MNHN). Figures 15, 16, 24, 50, 150–152.

Oocorys abyssorum (Verrill & S. Smith, 1884), SE Atlantic, Vema sta. CP02, 11°00'N, 45°15'W, 5073 m (MNHN). Figure 66.

Oocorys bartschi Rehder, 1943, Pequegnat 68 A13 sta. 22, 27°38'N, 95°22'W, 476 m (MNHN). Figure 119.

Oocorys umbilicata Quinn, 1980, Gulf of Mexico, 21°30.3'N, 96°11.7'W, 2245 m (MNHN). Figure 118.

Galeodea echinophora (Linné, 1758), Mediterranean, Golfo di Genova, Sori, 35–55 m (SMNH 476). Figures 17, 18, 22, 51.

Galeodea echinophora, Mediterranean, Corsica, off Calvi, 50–70 m (SMNH). Figure 120.

Cypraecassis testiculus (Linné, 1758), larva, Dana sta. 1286: V, 15°17'N, 61°29'W, plankton (ZMC). Figures 23, 115–117.

Semicassis granulatum (Born, 1779), Mediterranean, Golfo di Genova, Sori, 20–30 m (SMNH 475). Figures 19, 20.

Semicassis sp. aff. *granulatum* (Born, 1778), Dana sta. 1353, 33°51'N, 66°43'W, plankton (ZMC). Figures 63, 64.

Semicassis granulatum, no loc. (SMNH). Figure 65.

Semicassis saburon (Bruguière, 1792), N'Diago sta. 5, 17°26'N, 16°39'W, 500 m (MNHN). Figure 21.

PISANIANURINAE

Pisanianura grimaldii, New Caledonia, Biocal sta. DW51, 23°05'S, 167°45'E, 680–700 m (MNHN). Figures 25, 26, 55, 68.

Pisanianura grimaldii, Biocal sta. DW51, 23°05'S, 167°45'E, 680–700 m (MNHN). Figure 95.

Pisanianura grimaldii, R/V Vauban sta. CH22, 12°27'S, 40°10'E, 680–700 m (MNHN). Figures 94, 127.

Pisanianura grimaldii, holotype, Azores (MOM), 27.6 mm. Figure 126.

Pisanianura breviaxe, Biocal sta. CP52, 23°06'S, 167°47'E, 540–600 m (MNHN). Figures 27, 123, 153, 154.

Pisanianura breviaxe, holotype, off Kochi Pref., Japan (NSMT Mo 38611). Figure 124.

Pisanianura inflata (Brocchi, 1814), Pradalbino, prov. Bologna, Italy, Pliocene, deep-water deposits (Coll. della Bella). Figures 93, 125.

Kaiparanura spiralis (Marshall, 1918), holotype (NZGS Tm 6921), Pakaurangi Point, Kaipara Harbour, New Zealand, Altonian or more probably Ofaian age (Lower Miocene, A. Beu, pers. comm.). Figures 144, 145.

Kaiparanura spiralis, 1 mile NW of Pakaurangi Point, Kaipara Harbour, New Zealand (NMNZ M 81338). Figures 142, 143.

RANELLINAE

Argobuccinum pustulosum tumidum (Dunker, 1862), small specimen, 12 mm high, Waihau Bay, Cape Runaway (NMNZ 15045). Figures 52, 69, 86.

Fusitriton magellanicus (Röding, 1798), Patagonia, Puerto Pantalon, low tide (SMNH 663). Figure 53.

Fusitriton magellanicus, Portobello Canyon, ENE of Taiaroa Head, New Zealand, 540 m (NMNZ 9196). Figure 85.

Ranella olearia (Linné, 1758), Biacores sta. 41, 37°44'N, 29°04'W, 450–475 m (MNHN). Figures 31, 32.

Ranella olearia, Balgim sta. CP25, 36°41.5'N, 07°19.4'W, 544 m (MNHN). Figures 87, 88.

Ranella australasia (Perry, 1811), off Newcastle, NSW, Australia, 33°20'S, 152°17'E, surface plankton (AMS C 147218). Figures 30, 89.

NEPTUNELLINAE

Sassia kampyla (Watson, 1885), ENE of Taiaroa Head, 542 m, young specimen, height 6.9 mm (NMNZ 9196). Figure 28.

Sassia parkinsonia (Perry, 1811), Twofold Bay, NSW, height of shell 25 mm (AMS C 50074). Figure 29.

Sassia raulini (Cossmann & Peyrot, 1923), Chattian, Upper Oligocene of Bassin de l'Adour, coll. Lozouet (MNHN). Figure 90.

Sassia textilis (Tate, 1898), Muddy Creek, Hamilton, Victoria, Miocene (AMS C 146536). Figure 91.

Sassia remensa (Iredale, 1936), E of Lady Musgrave Id., Queensland, 23°52'S, 152°42'E, 296 m (AMS C 147348). Figure 92.

Charonia, larva, Dana sta. 1247:II, 17°57'N, 72°51'W, plankton (ZMC). Figures 37, 67, 99.

Charonia lampas (Linné, 1758), Conil, S Spain, from fishermen (SMNH). Figures 39, 40.

Cabestana cutacea (Linné, 1767), Messina, Sicily (SMNH 655). Figures 35, 54.

Cymatium, larva, Dana sta. 3940:Ia, 08°24'S, 42°54'E (ZMC). Figures 38, 70, 100.

Cymatium, larva, Dana sta. 3940:Ib, 08°24'S, 42°54'E (ZMC). Figure 34.

Cymatium, larva, Dana sta. 1253:V, 17°43'N, 64°56'W, plankton (ZMC). Figures 36, 98, 104.

Cymatium, young larva, Dana sta. 1337, 29°36'N, 64°01'W, plankton (ZMC). Figure 97.

Cymatium muricinum (Röding, 1798), Hawaii, coral reef at Honolulu (SMNH 649). Figure 33.

Cymatium problematicum Dautzenberg & Fischer, 1906, Gran Canaria, 15 m (SMNH). Figure 101.

Cymatium sp., Madeira, Eugenie Expedition (SMNH). Figures 102, 103.

PERSONIDAE

Distorsio reticularis (Linné, 1758), New Caledonia, 19°06'S, 163°10'E, 50 m (MNHN). Figure 122.

Distorsio clathrata (Linné, 1758), no data (SMNH). Figures 146, 147.

Distorsio sp., Philippines, Musorstom 3 sta. 117, 12°31'N, 120°39'E, 92–97 m (MNHN). Figure 84.

Distorsionella lewisi (Beu, 1978), New Caledonia, Biocal sta. DW66, 24°55'S, 168°22'E, 505–515 m (MNHN). Figure 121.

LAUBIERINIDAE

Laubierina sp., recently metamorphosed young, Mozambique Channel, Benthedi sta. 87, 11°44'S, 47°35'E, 3716 m (MNHN). Figures 41, 42, 56, 71, 162.

Laubierina sp., young, Caribbean, 21°35'N, 96°54.6'W, 937 m (MNHN). Figures 130, 131.

Laubierina peregrinator, Mozambique Channel, Benthedi sta. CH13, 12°13'S, 46°40'E, 2300–2500 m (MNHN). Figures 43, 44, 128, 129, 159–161.

Laubierina sp., the Azores, Biacores sta. 195, 37°56'N, 24°49.5'W, 1700–1776 m (MNHN). Figures 105, 107, 108.

Laubierina sp., Madeira sta. 13, 32°34'N, 17°07'W, 1970 m (MNHN). Figure 106.

Laubierina sp., New Caledonia, Biocal sta. DW48, 23°00'S, 167°29'E, 775 m (MNHN). Figure 96.

Akibumia orientalis, USBF sta. 4919, Kagoshima Gulf, Japan, 800 m (USNM 206835). Figures 45, 72, 136.

Akibumia orientalis, off Sydney, 33°36'S, 152°05'E, 1106–1143 m (AMS C 150223). Figures 46, 57, 157, 158.

Akibumia orientalis, holotype (ZMA 3.02.041). Figures 137, 138.

Akibumia schepmani, off S Queensland, 28°01'S, 153°59'E, 550 m (AMS C 150192). Figures 47, 48, 155, 156.

Akibumia flexibilis, Japan (ANSP). Figure 109.

Akibumia flexibilis, syntype (coll. Kuroda). Figure 140.

Akibumia schepmani, holotype (ZMA 3.62.001). Figure 139.

Akibumia flexibilis, Latham Id., S of Zanzibar, 06°52'S, 39°54'E (USNM 718939). Figure 141.

EPITONIIDAE

Akibumia reticulata Habe, 1962 (now Epitoniidae, provisionally *Epitonium*), holotype (NSMT M 39818). Figure 83.

Reproductive Systems of Neritimorph Archaeogastropods from the Eastern Pacific, with Special Reference to *Nerita funiculata* Menke, 1851

by

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Abstract. Differences in reproductive anatomy occur among the eastern Pacific neritimorphan gastropod genera. These differences are based on the location of the accessory sperm sacs in the female and the nature of the copulatory organ in males. Also, there appears to be a direct relationship between the spermatophoric filament and the length of the duct to the receptaculum seminis. In addition, a sorting mechanism has been demonstrated to occur within the crystal sac of *Nerita funiculata*.

INTRODUCTION

The Neritimorpha have a nearly world-wide distribution but as a group it is mostly limited to subtropical and tropical habitats. According to RUSSELL (1941) temperature is probably the limiting factor in the distribution of species from this suborder. Much of the systematic and anatomical work has been on the neritimorphs of the eastern and western Atlantic and the Indo-Pacific (ANDREWS, 1937; BERGH, 1890; BOURNE, 1908; FRETTER, 1946, 1965, 1966; LENSSEN, 1899; STARMÜHLNER, 1969, 1976, 1983; THIELE, 1902, 1929). Studies on the eastern Pacific neritimorphs have been neglected because the United States Pacific coast lacks a tropical fauna and, until recently, access to many of the tropical west American habitats has been difficult. According to KEEN (1971) only eight species of neritimorphs belonging to five genera have been described from the tropical eastern Pacific. Most of the morphological studies on eastern Pacific prosobranchs have been on caenogastropods from the Gulf of California (HOUSTON, 1976, 1985).

It is, therefore, valuable to study the reproductive systems of these eastern Pacific species in order to compare them to the genitalia of previously studied species. Also important is close examination of the anatomy and function of the spermatophores and such female organs as the crystal sac and capsule gland. These organs were previously studied by ANDREWS (1933, 1935, 1937) in several species of western Atlantic neritids. The species examined in the present study are *Nerita scabricosta* Lamarck, 1822, *Nerita funiculata* Menke, 1851, *Neritina latissima* Broderip, 1853, *Theodoxus luteofasciatus* Miller, 1879, and *Titiscania limacina* (Bergh, 1875). According to KEEN (1971), both *N. funiculata* and *T. luteofasciatus* occur throughout the Gulf of California and southward to Peru. *Nerita scabricosta* is also found throughout the Gulf of California but extends only as far south as Equador. *Titiscania limacina* is uncommon but has been observed from the northern Gulf of California to Panama. In contrast, *Neritina latissima* does not occur within the Gulf of California but ranges from Equador to only as far north as Acapulco, Mexico.

MATERIALS AND METHODS

Living specimens were collected from the following areas: *Nerita funiculata,* Coloradito, Baja California Norte; *Nerita scabricosta,* Puertecitos, Baja California Norte, Puerto Peñasco, Sonora, and Punta Chivato, Baja California Sur; and *Theodoxus luteofasciatus,* Bahía Concepción, Baja California Sur. Specimens of *Neritina latissima,* Isla del Coco, Costa Rica, and *Titiscania limacina,* San Carlos, Mexico, were studied using material loaned by the Los Angeles County Museum of Natural History. Descriptions of the genitalia were made after careful dissections of both preserved and living material (preserved only for *Neritina* and *Titiscania*); stained sections were examined in order to elucidate cellular details. The soft parts were relaxed in propylene phenoxytol (OWEN, 1955) and fixed in Bouin's

fluid. Sectioned material was then stained with Korn-houser's hemalum, eosin B, and Alcian blue. Ciliary currents were observed by using suspended carmine particles in seawater.

RESULTS

Nerita funiculata

The male duct (Figure 1A): In living males the testis is bright orange and shares the visceral mass with the digestive gland. From the testis a thin-walled straight gonadal vas deferens runs down the right side of the digestive gland until it reaches the posterior end of the pallial duct. Here it becomes highly convoluted and glandular. During the breeding season, which occurs from late spring through summer, the vas deferens is packed with spermatozoa and functions as a seminal vesicle. This tube enters the pallial duct ventrally about one-third of the distance along its length.

In this species the pallial duct is suspended from the right wall of the mantle cavity. In addition, in living specimens it appears as an elongate white glandular mass that is closed throughout its entire length. Histological sections reveal that it is really two separate glands, an anterior prostate and a posterior auxiliary gland. The anterior one-half of the prostate is composed of numerous acini that are lined with alternating ciliated and eosinophilic staining gland cells. Posteriorly these cells give way to basophilic staining cells. However, just before entering the auxiliary gland there are two lateral strips of mucous cells. In this region the seminal vesicle becomes the pallial duct. The lumen of the prostate bifurcates, sending one branch posteriorly while the other switches back in an anterior direction. In the auxiliary gland the cells stain bright red and are filled with many small spherical inclusions. There are no ciliated cells in this region.

The genital opening lies dorsal to and well in front of the anus. It is lined with ciliated cells alternating with mucous cells and is surrounded by a thin sheet of circular muscle fibers. In this species the penis is a dorsoventrally flattened triangular flap situated between the cephalic tentacles and attached along its posterior edge. A ciliated groove begins at the tip and runs along the right side of the organ until it disappears into a small pouch at the base. In living individuals the genital aperture can be observed lying close to the base of the penis, although there is no direct connection.

The male gametes are stored in spermatophores, which are transferred to the female during mating. These structures measure 2 to 2.5 mm in length and have a fusiform body that is blunt at one end. As shown in Figure 2, a long filament arises from the rounded end and is wrapped around the body in a spiral fashion. Cross sections show the filament to be hollow.

The female duct (Figure 3A): The female system of this species is diaulic with both nidamental and genital open-ings lying adjacent to one another next to the anus. Between the nidamental opening and the anus there is a flap of tissue that acts as a valve that closes off the former during the release of fecal pellets. In living individuals the white ovary occupies almost the entire visceral mass during the summer mating season. From the ovary a ciliated, thin-walled oviduct winds down the right side of the visceral mass and joins the posterior region of the pallial oviduct. Just before entering the pallial region there is a small opening from the oviduct into the mantle cavity. In mature specimens the large cream-colored capsule gland extends from just beneath the mantle edge to the extreme posterior region of the mantle cavity. As in males, the pallial oviduct is suspended from the right mantle wall. The nidamental opening is lined with low columnar ciliated cells. Just posterior to this opening there is a bifurcation with one duct leading to the capsule gland and the other to the crystal sac. This sac is a thin-walled, bulbous pouch that begins on the right side of the capsule gland and swings over onto the dorsal surface. The anterolateral wall of this organ is lined with mucous cells that constitute a mucous pad. The medial wall is lined with low columnar cells from which arises a ciliated groove that runs dorsad into the proximal region of the sac. Here, this groove opens directly into the ventromedial wall that is thrown into a series of complex ciliated folds (Figure 4). The functions of these folds will be discussed later. The dorsolateral wall is smooth and non-ciliated.
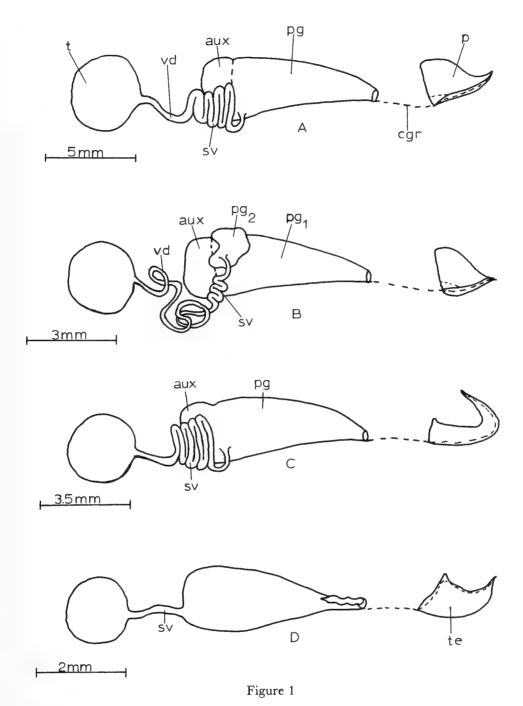
The ciliated lumen of the voluminous capsule gland appears as a dorsoventral crescent with the concave side facing left. The staining characteristics of this organ are as follows:

Cell Type I—Subepithelial eosinophilic gland cells with round basal nuclei. These cells occur in clusters that open into the lumen via common ducts. Moreover, these cells constitute the ventral and lateral walls of the entire capsule gland.

Cell Type II—These cells have flat basal nuclei and a colorless cytoplasm. In addition, they are arranged as acini and lie dorsal to the lumen.

Cell Type III—Mucous cells that are sandwiched between the lumen and cell type II.

Figure 5 is a diagram of the ciliary currents within a capsule gland that was opened along the mid-dorsal line. About two-thirds of the way through the capsule gland the lumen divides into two lateral branches. In this region the right branch becomes the posterior end of the capsule gland while the left leads to the albumin gland. In the albumin gland a fourth cell type that stains turquoise with Alcian blue occurs. This gland is bilobed and is referred to as the upper and lower albumin glands. In the lumen of the lower albumin gland there is a ventral ciliated groove that bifurcates, with one branch leading to the oviduct and the other to the fertilization chamber. This sac is really

Figure 1

Diagrammatic reconstructions of the male genital ducts. A. *Nerita funiculata* and *Nerita scabricosta*. B. *Theodoxus luteofasciatus*. C. *Neritina latissima*. D. *Titiscania limacina*. aux, auxiliary gland; cgr, ciliated groove; p, penis; pg, prostate gland; sv, seminal vesicle; t, testis; te, tentacle; vd, vas deferens.

an expanded, thin-walled region of the receptaculum seminis. The walls opposite the fertilization chamber are composed of numerous acini lined with tall columnar cells. These acini empty into a ciliated trough that opens directly into the fertilization chamber and that also communicates with the duct to the spermatophore sac. In cross section the acini appear circular and are packed with sperm oriented with their heads toward the center and their tails attached to the epithelium. In addition, the receptaculum seminis also seems to function as an ingesting gland, for pieces of spermatozoa can be observed with vacuoles of some of the acinar epithelial cells. A convoluted duct leaves

this organ and continues in an anterior direction for some distance, then abruptly switches back to enter the spermatophore sac. This elongate muscular pouch is about one-half the length of the capsule gland and is full of spermatophores in mating individuals. Near its proximal end is the opening to the long muscular sperm duct, which runs anteriorly and terminates at the genital pore.

For the following species only major differences in their anatomy will be noted.

Nerita scabricosta

The only noteworthy difference for this species is the absence of an opening to the mantle cavity from the posterior region of the oviduct (Figure 3B, see arrow). Otherwise the reproductive systems are essentially the same as for the previous species.

Theodoxus luteofasciatus
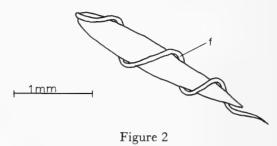
The male duct (Figure 1B): (a) A second prostate gland seems to lie between the seminal vesicle and the anterior prostate. (b) The seminal vesicle is much larger than in Nerita and it also differs in being proximally coiled.

The female duct (Figure 3C): (a) A separate duct joins the albumin gland with the spermatophore sac. (b) The receptaculum seminis is a small bulbous organ located at the end of a long duct that leads directly to the albumin gland.

Neritina latissima

The male duct (Figure 1C): (a) The most noteworthy difference is the morphology of the copulatory organ. The penis, instead of being a triangular flap, is cylindrical and distally tapers to a point. A ciliated groove begins just proximal to the tip and continues posteriorly along the dorsal surface to the head where it ends just behind the right cephalic tentacle. In addition, a flap of tissue can be observed covering this groove except for the extreme distal end. (b) The spermatophores are similar to those of Nerita except that the filaments are much shorter.

The female duct (Figure 3D): The histology for this species is similar to that of Nerita. However, there are some major differences in the gross anatomy. (a) The system is triaulic with the presence of a ductus enigmaticus. This duct, originally described by BOURNE (1908), branches off the sperm duct just anterior to where the duct from the receptaculum joins the spermatophoric duct. This convoluted canal can be seen as it passes forward alongside the capsule gland and then straightens out distally just before opening into the mantle cavity. (b) The spermatophore sac is spherical and is only about one-fourth the length of the capsule gland. Up to four spermatophores were observed inside this organ. (c) The duct that joins the spermatophore sac to the receptaculum seminis is straight and short. (d) There is no opening from the go-

Figure 2

A spermatophore from Nerita funiculata. f, filament.

nadal oviduct into the mantle cavity. (e) The crystal sac, which appears to be filled primarily with sand grains, lies on the left side, dorsal to the distal region of the capsule gland.

Titiscania limacina

The male duct (Figure 1D): (a) The seminal vesicle is straight, not convoluted. (b) No accessory prostate gland was observed. (c) The genital opening is bordered by two tissue flaps that lead to a ciliated groove that passes to the right side of the head. (d) There is no separate penis. However, the right cephalic tentacle is enlarged and may function as the intromittent organ.
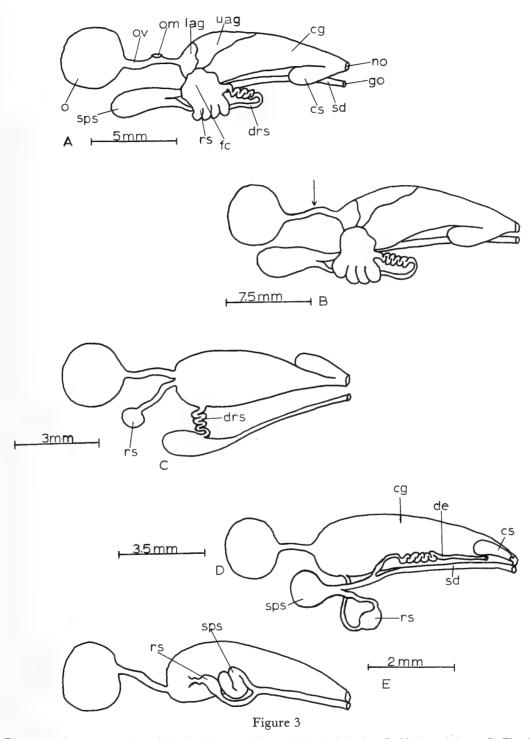
The female duct (Figure 3E): (a) The spermatophore sac is elongate and S-shaped. (b) The ductus enigmaticus and crystal sac are absent. (c) The receptaculum seminis is a rather large tear-drop shaped organ, which lies just posterior to the spermatophore sac. (d) The duct that joins the receptaculum seminis with the spermatophore sac is short, like that found in Neritina.

Reproduction in Nerita funiculata
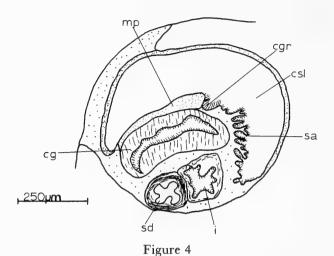
The reproductive season for this species was from the last of May through September. During this time there was both extensive mating and spawning. However, during the winter months spermatozoa have been seen in the receptaculum seminis of females. Therefore, spawning individuals could possibly have mated during some prior season.

The entire mating process takes anywhere from 10 minutes to one-half hour, depending on the individual pair. Initially, the male climbs onto the right side of the shell of the female and inserts the penis into the right side of the mantle cavity. During this time the pair makes back and forth movements and simultaneously rotate to and fro through a 90 degree arc. After pausing for a period of about one minute they oscillate in the opposite direction. At this time the spermatophores are transferred to the mantle cavity of the female. When copulation is completed the male either crawls down and away or withdraws into the shell and falls off.

The egg capsule: The yellowish-white capsule is elliptical in outline and measures up to 3 mm across the long axis.

Figure 3

Diagrammatic reconstructions of the female genital ducts. A. *Nerita funiculata*. B. *Nerita scabricosta*. C. *Theodoxus luteofasciatus*. D. *Neritina latissima*. E. *Titiscania limacina*. cg, capsule gland; cs, crystal sac; drs, duct to receptaculum seminis; de, ductus enigmaticus; fc, fertilization chamber; go, genital opening; lag, lower albumin gland; no, nidamental opening; o, ovary; ov, oviduct; om, opening of oviduct into mantle cavity; rs, receptaculum seminis; sd, sperm duct; sps, spermatophore sac; uag, upper albumin gland.

Figure 4
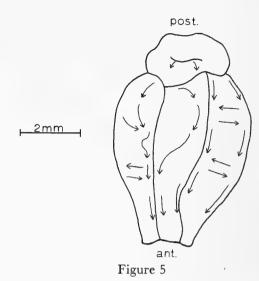
A cross section through the crystal sac from a female *Nerita funiculata.* cg, capsule gland; cgr, ciliated groove; csl, lumen of crystal sac; i, rectum; mp, mucous pad; sa, sorting area; sd, sperm duct.

Figure 5

Ciliary currents within a capsule gland from *Nerita funiculata.* ant., anterior; post., posterior.

It is composed of a lens-shaped cap sutured to a flat base that is affixed to the substratum. As shown in Figure 6, the capsule is composed of two layers. The inner homogenous layer has the same staining properties as the secretions of the capsule gland. The outer layer is a mucous coat in which are embedded spherulites. The base has the same staining qualities as the homogenous layer, except it is filled with mucous vesicles. The eggs, up to 50 in each capsule, are suspended within an albuminous secretion.

As the egg capsules are released they are sprinkled with spherulites which were stored in the crystal sac. These particles are extracted from fecal pellets as they pass from the anus. Sections of the gut reveal a heterogenous assortment of particulates in the feces, including a variety of diatom skeletons. As this material is released from the anus into the mantle cavity, a portion is carried by cilia to the crystal sac where it is sorted and stored. On entering the sac this material becomes entangled in mucus that is secreted by the mucous pad (Figure 4). Here, this mucous string passes to the sorting area where only spherical particles are selected out while the waste is cleared back into the mantle cavity. Dissections of the crystal sac also show that most of these spherulites are of similar size. When needed, they are passed along the ciliated groove (mentioned earlier) to the outside where they become embedded in the surface of the egg capsule. Up to four layers of spherulites occur in the outer wall.

DISCUSSION
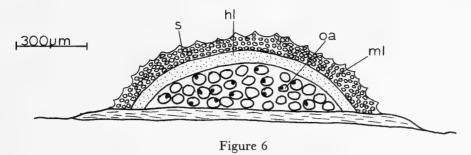
The general anatomy of reproductive systems is rather uniform among neritimorph prosobranchs. This has been substantiated in the definitive works by ANDREWS (1937) and BOURNE (1908). Moreover, in all of the species investigated in this study, the male genitalia produce spermatophores that are subsequently transferred to the female by a cephalic penis or some equivalent structure. In the female the spermatophores are stored in a bursa or spermatophore sac where the sperm are released and travel to the receptaculum seminis prior to fertilization. This is also the case for other neritimorphs (BERRY *et al.*, 1973; BOURNE, 1908; FRETTER, 1946, 1984; STARMÜHLNER, 1969, 1976, 1983). Although spawn was observed only for *Nerita funiculata,* its hemispherical structure is in accordance with that of other neritids, as described by ANDREWS (1935) and FRETTER (1946). Even though these similarities exist, differences are apparent in the reproductive anatomy at the generic level. Both BOURNE (1908) and ANDREWS (1937) remarked on the relationships among genera based on similarities in their anatomy. A more recent study on the anatomy of *Nerita birmanica* (Phillipi, 1844) by BERRY *et al.* (1973) has confirmed the results of the aforementioned early works. In addition, STARMÜHLNER (1969, 1976, 1983) has shown this to be true for the freshwater and brackish *Clithon, Neritina,* and *Septaria* from various localities throughout the Indian ocean.

In the species studied, some obvious differences between *Nerita, Theodoxus* and *Neritina* have not been previously mentioned. In *Nerita* the receptaculum is directly attached to the surface of the albumin gland. Internally a ciliated groove leads from the receptaculum to the fertilization chamber. In *Neritina* and *Theodoxus,* however, the receptaculum seminis is separate and is connected to the albumin gland by a well defined duct. This also appears to be the case for the Indo-Pacific neritids observed by STARMÜHLNER (1976). Furthermore, he shows that in *Neritina* and *Septaria* the bifurcation that gives rise to the duct to the receptaculum seminis occurs about halfway along the length of the sperm duct. This differs from *Neritina latissima* (and *Titiscania*) where the branching is proximal and just anterior to the spermatophore sac.

Figure 6

Cross section of an egg capsule from *Nerita funiculata*. hl, homogenous inner layer; ml, outer mucous layer; oa, fertilized eggs; s, spherulites.

STARMÜHLNER (1976, 1983) also noted that the reproductive systems of *Neritilia* are not as complex as those in other neritids. Species in this genus are lacking both the ductus enigmaticus and the duct that joins the receptaculum seminis to the sperm duct. In addition, the spermatophore sac is a simple elongated pouch. Moreover, *Neritilia* is usually placed in a separate subfamily of the Neritidae.

Curiously, neither a crystal sac nor a separate penis was observed in *Titiscania*. In an earlier study on *T. limacina*, MARCUS & MARCUS (1967) observed a small empty sac attached to the anterior end of the pallial oviduct. Because no spawning was observed, it was only speculated that the sac functioned as a crystal or reinforcement sac. In addition, they mentioned the presence of multiple copulatory bursae in the female. These structures were not observed in specimens during my study. Unfortunately only females were collected during their study so the male genital tract was not described. Further anatomical work needs to be done on the anatomy of *Titiscania* to clarify its systematic position among the Neritimorpha. Presently the genus is placed in its own family. For the family Neritidae, the presence of a crystal sac appears to be an autopomorphic character.

ANDREWS (1937) described the spermatophores from several species of neritids and noted a wide variability in form, including the length of the spermatophoric filament. She also mentioned that these filaments serve as conduits for sperm transfer to the receptaculum seminis. This, however, contrasts with the finding by FRETTER (1984) for *Phenacolepas*. Here the sperm are liberated from the spermatophores directly into the lumen of the bursa or spermatophore sac. Moreover, there appears to be a relationship between the filament length and the nature of the duct to the receptaculum seminis. In *Nerita* and *Theodoxus* the spermatophoric filaments are longer than those found in *Neritina* or *Titiscania*. The same holds true for the duct joining the receptaculum seminis to the spermatophore sac or, as in *Theodoxus*, to the albumin gland.

From the examination of stained sections and ciliary currents within the genitalia of *Nerita funiculata*, the following sequence of events during and after mating can be inferred. During copulation the spermatophores enter the genital opening and are moved by peristalsis up the sperm duct and stored in the spermatophore sac. Stained sections reveal spermatophoric filaments in the lumen of the duct that leads to the receptaculum seminis. Hence, the spermatozoa apparently travel to the receptaculum through these filaments. This has been suggested for other species of neritids (ANDREWS, 1937; BERRY *et al.*, 1973). As was previously mentioned, the sperm are then stored in the receptaculum until they are utilized for fertilization. The empty spermatophores appear to be ingested by the epithelial cells that line the wall of the spermatophore sac. Sections reveal left-over fragments surrounded by secretory droplets. The ova travel down the oviduct and enter the fertilization chamber by way of the ventral ciliated groove. Here they are apparently fertilized by sperm released from the receptaculum. These fertilized eggs then pass through and are mixed with secretions from the albumin glands. Anteriorly they enter and pass through the capsule gland where they become coated with secretions produced by the subepithelial gland cells in this region. These secretions constitute the egg capsule, which hardens when it passes through the nidamental opening to the outside.

In many species of neritids the walls of egg capsules are reinforced by inorganic particles (ANDREWS, 1933, 1935; FRETTER, 1946). Moreover, these reinforcements consist of different substances. In *Nerita*, for example, these particles are spherulites consisting primarily of calcium carbonate. According to ANDREWS (1935) they are apparently synthesized in the digestive gland. There is, however, no evidence of spherulite formation in the digestive glands of the neritids in this study. Since both *Nerita funiculata* and *Nerita scabricosta* live on limestone reefs, it is possible that minute particles of lime are scraped up along with the food by the radula. As they pass through the gut they are modified and become spherical. For *Neritina* and *Theodoxus* the egg capsules are impregnated mostly with sand. However, diatom skeletons and sponge spicules also occur in the capsules of these genera (ANDREWS, 1935). No spawn was observed for *Titiscania*.

The present study gives the first evidence of a sorting mechanism in the crystal sac of *Nerita*. A possible advantage in using similar size particles to reinforce and harden the capsule wall would be to provide a relatively smooth

surface to minimize the effects of waves and currents. There is no evidence of sorting mechanisms in the crystal sacs of *Theodoxus* or *Neritina*. Because these species use primarily sand to strengthen their egg capsules, a sorting would not be needed, as sand is usually already sorted by currents and waves. However, more work is needed to clarify this and other issues, such as the exact site of fertilization and the mechanism by which spermatophores are transferred from male to female.

Until recently the Neritimorpha were considered to be intermediate between the Archaeogastropoda and the Caenogastropoda because of their shared characters with the latter group (BOURNE, 1908; FRETTER, 1965, 1984). However, HASZPRUNAR (1988) has provided strong arguments for placing the Neritimorpha lineage even before the Vetigastropoda. This is based in part on previous studies concerning their special mode of shell formation, discussed by THOMPSON (1980), and differences in their sperm morphology (HEALY, 1988). If HASZPRUNAR (1988) is correct, the advanced characters exhibited by neritimorphs, including those of their genitalia, arose several times and can be considered convergences.

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Indirect Evidence of a Morphological Response in the Radula of *Placida dendritica* (Alder & Hancock, 1843) (Opisthobranchia: Ascoglossa/Sacoglossa) to Different Algal Prey

by

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Abstract. Examination of radulae from the ascoglossan mollusk *Placida dendritica* (Alder & Hancock, 1843) collected in New Zealand, Australia, Japan, and west coast North America revealed two morphological types. Each was correlated with the type of alga from which the slugs were collected. Those feeding on perennial *Codium* had smaller teeth, more teeth, and a tight radular coil in an enlarged ascus. Those feeding on seasonal *Bryopsis* and *Derbesia* had larger teeth, fewer teeth, and only a slightly curved radular ribbon (never a coil) in the ascus. This apparent morphometric response of radular structure to algal structure and defenses may explain similar sporadic size discrepancies observed in populations of three other ascoglossan genera, *Alderia*, *Elysia*, and *Limapontia*.

INTRODUCTION

For several species of ascoglossans, the radular teeth can, numerically and morphologically, (1) vary ontogenetically within an individual; (2) vary seasonally within one species; (3) have a reversal of the normal process of producing sequentially larger teeth; and (4) vary in the rate of tooth production as determined by comparing body lengths to the total number of teeth (RAYMOND & BLEAKNEY, 1987; BLEAKNEY, 1988). This paper reports a fifth category that had not previously been suspected, namely that the size of and production rate of teeth can vary in response to the type of algae eaten. Presumably this is a response to the degree of mechanical difficulty in penetrating algal filaments and to the effort required to suck out the cell sap.

BLEAKNEY (1989) recently demonstrated consistency over much of the Pacific Basin in the ultrastructure of the cutting edge of teeth of *Placida dendritica*. However, he noted in particular a perplexing lack of direct relationship between body size and total number of teeth. In most cases the largest animals, 14–20 mm in length, had fewer teeth than many animals only 3–4 mm in length. He concluded that this discrepancy was a reflection of either long geographic isolation and had a genetic basis, or was merely a temporal extreme such as he had observed in Nova Scotia populations of *Elysia chlorotica* Gould, 1870 (RAYMOND &

BLEAKNEY, 1987). However, after examining a series of *P. dendritica* from Oregon, a third and more plausible explanation is now available.

MATERIALS

Dr. Cynthia Trowbridge sent me three separate lots of *Placida dendritica* collected from three species of alga—*Codium fragile* (Suringar) Hariot, *Codium setchellii* Gardner, and *Bryopsis corticulans* Setchell—in the hopes that I might discover radular differences. She felt that differences in the general appearance and behavior of *Placida* on these algae indicated possible specialization and speciation. However, and without exception (based on examination of 10 slugs from each alga), the pronounced morphological variation observed fell into only two categories and these were directly correlated with the two genera of algae. These observations prompted a re-examination of my notes and collections of *P. dendritica* from British Columbia, Japan, Australia, and New Zealand, and some of those data are included in Figure 1.

RESULTS

In every case, the largest animals had been collected from *Bryopsis* or the related genus *Derbesia*. The radular ribbon
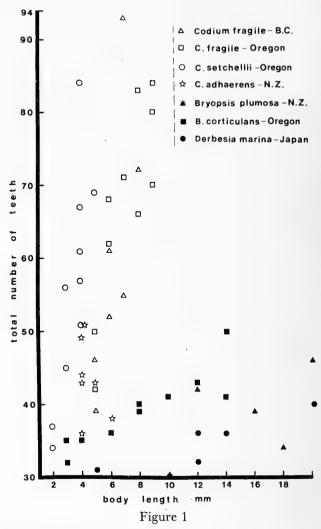
of *Bryopsis*-feeding *Placida dendritica* had fewer but much larger teeth and a slightly curved, descending radular limb (Figures 2, 3). In sharp contrast, slugs from *Codium* had many more teeth but much smaller ones (Figures 4, 5) and their strongly coiled descending radular limbs were already evident at body lengths of only 3 and 4 mm. Even with body lengths of 14 mm, slugs from *Bryopsis* had only a slightly curved ribbon in the ascus area.

Figures 2 to 5 are of two equally large buccal masses from two 8 mm *Placida dendritica,* photographed at the same magnification, yet the tooth bases in the ascending series of the *Bryopsis* feeder are at least twice as large as the *Codium* example. The differences in the size and number of teeth do not seem to effect the relative size of the buccal mass in the two categories, although a larger sample might emphasize an incipient divergence indicated by query arrows in Figure 6. The numerous additional teeth produced by the *Codium*-feeding slugs are accommodated outside the buccal mass within an enlarged ascus area.

DISCUSSION

Available morphological information indicates that *Placida dendritica* is a single species, at least within the Pacific Basin (BLEAKNEY, 1989). Among the three collections from Oregon, there were no differences in the ultrastructure of the serrated edge of the radular teeth. If *P. dendritica* actually consisted of a *Codium*-species and a *Bryopsis*-species, one would expect real differences in the teeth reflecting the considerable differences in structure of the two algae. The only radular differences detected were the relative size of teeth and the total number of teeth, two variables common to any population. That these two variables, as well as the category of maximum body size, were directly related to the different algal prey is significant. That the two algal genera were *Codium* and *Bryopsis* is equally significant for the former is perennial (pseudoperennial) and the latter highly seasonal. Perennial or pseudoperennial plants should (as predicted by evolutionary theory) partition more resources into anti-herbivore defenses. This becomes manifest as degrees of edibility and digestability, and ultimately affects the growth rates of predators. CLARK & DEFREESE (1987) emphasized the strong evolutionary interplay of algal life histories, physiology, and structure with that of alga-sap-sucking ascoglossans.
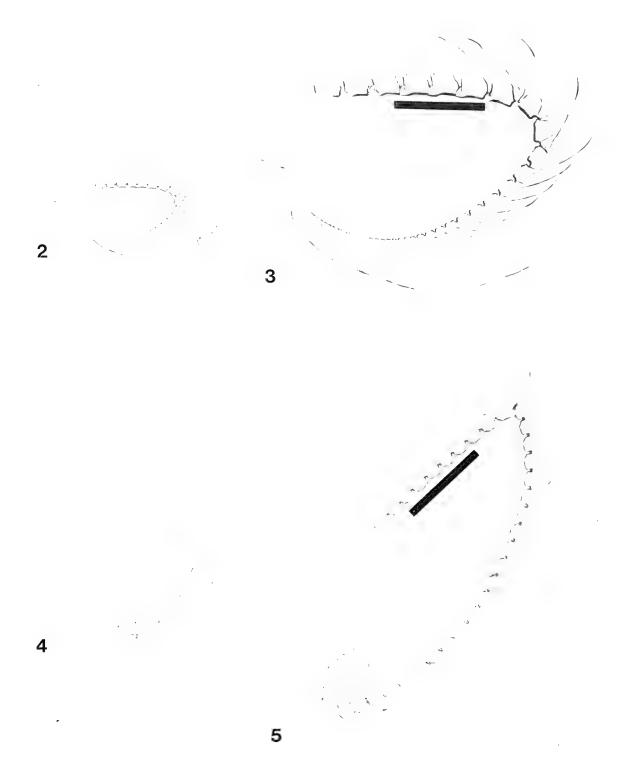
Because *Codium* is a perennial, it undoubtedly has developed defenses to reduce grazing efforts of ascoglossans, which are generally directed at the coenocytic filaments of siphonaceous algae because one puncture by a radular tooth gains access to the entire thallus system. Access to *Codium* must be frustrated in part by its peculiar surface which consists of a carpet of erect, compacted, clavate, utricles whose exposed apices are capped by a lamellate cuticle (WOMERSLEY, 1984). These utricle subunits almost amount to a septate condition, as the feeding slug must shift from one utricle to another to extract sap. Narrow radular teeth may be more effective than stout ones in penetrating this armor, but at the same time, under this

Figure 1

Relationship of body length and total number of teeth of *Placida dendritica* from various geographic regions to type of alga fed upon. *Codium* species are plotted as open symbols, and *Bryopsis/ Derbesia* are solid symbols.

repetitious puncturing of numerous utricles, the serrations may wear down faster and tips break off and pieces chip out (see photographs in BLEAKNEY, 1989).

The life history of *Bryopsis,* in contrast, involves a seasonal appearance of irruptive, transient populations with little necessity to evolve major protective toxins or mechanical barriers. The thin-walled, plumose thallus of *Bryopsis* may be most effectively penetrated and split open by a large diameter tooth, and certainly the amount of cell sap extracted per puncture must be far greater from *Bryopsis* than from *Codium*. The nutrient value is probably far higher as well, for as CLARK & DEFREESE (1987) pointed out, perennial algae tend to produce a spectrum of secondary metabolites whose toxic effects are not necessarily direct, but which may serve the alga by inhibiting (or slowing) growth and reproductive processes in the attacking ascoglossans.

2

3

4

5

Explanation of Figures 2 to 5
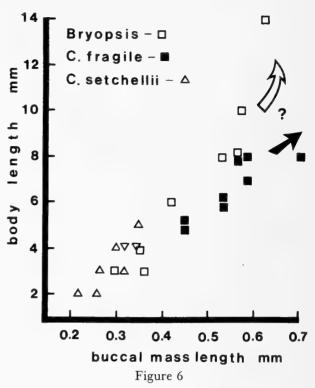
Figures 2, 3. Entire buccal mass and enlargement of the radular area of an 8-mm-long *Placida dendritica* found on *Bryopsis corticulans* in Oregon, July 1988. Scale bar = 80 μm.

Figures 4, 5. Entire buccal mass and enlargement of the radular area of 8-mm-long *Placida dendritica* found on *Codium fragile* in Oregon, July 1988. Scale bar = 80 μm.

JENSEN (1989) conducted feeding experiments utilizing *Elysia viridis* (Montagu) by transferring slugs found on *Codium fragile* to the cellular alga *Chaetomorpha linum* (Miller) Kutzing, and those found on *Chaetomorpha* to the coencytic *Codium*. In general, the slugs experienced great difficulty in changing their feeding habits, with time lags of up to two weeks. These time delays were attributed to learning periods but may have reflected in part the time necessary to restructure the radular apparatus. Unfortunately, the respective radulae were not examined and compared. However, as there are three regional populations of *Elysia viridis* in Europe, each feeding primarily on a different genus—*Codium, Bryopsis,* and *Chaetomorpha* (JENSEN, 1989)—any real difference in radular morphology could be verified prior to prolonged feeding experiments. In passing, it is worth noting that Jensen's *Codium*-derived *E. viridis* were smaller ($n = 17$; average length 1.45 cm) than those collected off *Chaetomorpha* ($n = 30$; average length 2.13 cm).

I suggest that the survival strategy of *Placida dendritica* is to prey upon a variety of algae, including reliable perennials and desirable transients. If the veligers settle upon *Codium* they must contend with defensive chemicals and structures, and the result is a relatively small body size, rapid production of slender teeth, and fewer eggs laid. If the veligers find *Bryopsis* instead, they grow rapidly, produce fewer, more massive teeth, reach body lengths twice that of the *Codium*-limited individuals, and produce far more eggs.

Such a biochemical interplay between alga and ascoglossan, involving defenses, feeding effort, and nutrient value could explain the startling size discrepancies that one encounters sporadically when sampling populations over extended time periods. For example, the European ascoglossan *Limapontia depressa* Alder & Hancock, 1862, is usually only 2–3 mm in length, but in August 1969, in the Isefjord, Denmark, the late Henning Lemche (*in litt.*) found a swarm of hundreds of spawning animals most of which were an exceptional 8 mm in length, and their egg masses contained 800–1000 eggs. In contrast, collections of specimens of the usual 2 mm size, gathered on the same day but at a different locality, had egg masses containing only 155 eggs. Similarly, in the Minas Basin, Nova Scotia, the ascoglossan *Alderia modesta* (Loven, 1844) can grow to 15 mm, nearly twice its "normal" size, but this happens at irregular intervals, often years apart. *Elysia chlorotica* is usually considered "large" at 20–30 mm, but on occasion, in Minas Basin tidal marshes, entire populations can reach 35–45 mm. GIBSON *et al.* (1986) reported an exceptional phenomenon concerning this species. Much of the local population in the summer of 1983 and 1984 was without chloroplasts. Apparently, viable chloroplasts from *Vaucheria* were unavailable, yet the slugs appeared healthy and were actively spawning. Most of the non-green *Elysia* were 6–12 mm in length and only the few green individuals attained larger body sizes.

Figure 6

Relationship of body length and length of buccal mass to type of alga fed upon by *Placida dendritica* from Oregon.

CONCLUSIONS

The above observations, considered with the ecological studies of CLARK & DeFREESE (1987), emphasize how entrained and responsive are the life histories and anatomies of ascoglossans to their algal prey. It is also evident that these responses are open to experimental verification and manipulation at laboratories where controlled culturing techniques are available for both larvae and algae. The standard method of testing of adult ascoglossans using algal choice situations to establish a food preference spectrum for a particular slug species could be misleading. The "preferred" food of adults may simply depend upon the alga that veligers or larvae first encountered and to which they effectively adapt morphologically and physiologically during their brief life history period.

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Trail Following in *Littorina irrorata*: The Influence of Visual Stimuli and the Possible Role of Tracking in Orientation[1]

by

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Abstract. The marsh periwinkle *Littorina irrorata* can detect and follow mucous trails previously deposited by conspecifics. Preliminary observations revealed that the tendency of *L. irrorata* to track may be influenced by the presence of visual directional stimuli. When tested in a field arena, both the frequency and degree of trail following exhibited by periwinkles were significantly higher under conditions in which the marker's trail was deposited in response to a visual stimulus. No significant differences were found between controls and treatments in which a visual orientational cue was absent for marker snails. These data suggest that mucous trails deposited by visually oriented marker snails differ in informational content from trails laid by non-oriented snails. Microscopic and elemental analysis of trails deposited by the same snail while crawling in the absence and presence of a directional stimulus revealed thin threadlike structures possibly involved in determining trail polarity, but no noticeable differences were observed in the overall physical or chemical structure of the two groups of trails.

INTRODUCTION

The influence of mucous trails on the movements and orientation of gastropods has received considerable attention, but most studies have focused on the role of trail-following behavior in limpet homing. The marsh periwinkle *Littorina irrorata* (Say, 1822), like many marine prosobranchs, frequently follows conspecific mucous trails in the same direction in which they were originally deposited (HALL, 1973). Although recent evidence suggests that trail following in this species increases locomotor efficiency by reducing the force required to crawl across the marsh substratum (TANKERSLEY, 1989), the role of intraspecific trails and trail polarity in determining the movements and orientation of *L. irrorata* in the marsh has yet to be demonstrated.

Littorina irrorata typically is active at low tide among stands of the cord grass *Spartina alterniflora* (BINGHAM, 1972; HAMILTON, 1978a) which the snails ascend when inundated by the advancing tide (HAMILTON, 1976). Although numerous shore-living gastropods have been shown to utilize a variety of orientational mechanisms and directional stimuli including light, gravity, water currents, and waves to determine their movements and maintain their patterns of distribution on the shore (UNDERWOOD, 1979), the zonal orientation and short-term movements of *L. irrorata* on the marsh substratum are largely mediated by local visual cues, especially grass stalks (HAMILTON, 1977a, 1978b; HAMILTON & WINTER, 1982). When displaced from its natural habitat onto bare sand, *L. irrorata* crawls toward areas of vegetation (HAMILTON, 1978b). Avoiding areas devoid of *Spartina* is particularly adaptive since snails locate and climb grass stalks and in so doing may avoid predators at high tide (HAMILTON, 1976; WARREN, 1985) and reduce heat stress (McBRIDE *et al.,* 1989). Because directional information present in *L. irrorata* trails lasts for at least 60 min following deposition (STIRLING & HAMILTON, 1986), trails deposited by conspecifics may provide information necessary for the relocation of plant stems during tidal inundation or serve as a supplement to other orientational guideposts, including visual cues.

Numerous studies have revealed that animals often possess redundant orientational mechanisms which facilitate the performance of the same tasks under different environmental conditions (ABLE, 1980). Because most previous examinations of trail following and orientation in *Littorina irrorata* have either employed visual stimuli (STIRLING &

HAMILTON, 1986; TANKERSLEY, 1989) or controlled for the potential influence of old trails on test surfaces (HAMILTON, 1977a, 1978b; HAMILTON & WINTER, 1982), it has been impossible to ascertain the role of conspecific trails in determining the orientation behavior of *L. irrorata* or explore any relationship that might exist between mucous trails and other directional stimuli, especially visual landmarks.

Examinations of the trail-following behavior of *Littorina irrorata* under controlled conditions revealed that when marker (trail-layer) snails were deprived of visual directional stimuli, the tendency of tracking *L. irrorata* to follow the marker's trail was substantially reduced. This observation suggested that trails of visually oriented snails might contain important trail-specific information, in addition to directional (polarity) information, that may not be present or detectable in the trails of non-oriented snails foraging or crawling randomly on the marsh substratum. The present study addresses the hypothesis that trails produced by visually orienting marker snails differ from those of non-visually orienting snails with respect to their potential to elicit trail following by tracker snails.

MATERIALS AND METHODS

General Procedures

Mature *Littorina irrorata* (shell length 17–23 mm) were obtained from marshes adjacent to the Florida State University Marine Laboratory, Turkey Point, Franklin County, Florida. Snails not used immediately after collection (see microscopic examination of trails) were maintained in plastic aquaria partially filled with natural seawater (32–34‰ salinity) under fluorescent light on a 12L:12D photoperiod. All snails were used within five days of collection.

Arena Experiments

Trail following by *Littorina irrorata,* in response to trails that had been deposited in the presence or absence of a visual directional stimulus, was assessed using an experimental arena resembling that of HAMILTON (1978b) (Figure 1; see TANKERSLEY, 1989, for a detailed description). The arena consisted of two 40-cm-diameter circular wooden platforms constructed of 1.9 cm thick plywood. A 30-cm-diameter glass plate was inserted into the center of the upper platform and served as the test surface. A 10 cm high white plastic collar was placed on top of the upper platform to limit the influence of external visual stimuli. The arena was then mounted on top of a PVC pipe and placed 1.3 m above the salt marsh substratum among stalks of *Spartina.*

Twenty pairs of marker and tracker *Littorina irrorata* were tested under four treatment combinations in which a visual stimulus (12 cm × 3 cm black vertical bar) either was attached at a random location on the inside of the collar (Present treatments) or removed (Absent treatments)

(Table 1). For each replicate, a marker snail was selected from the nearby salt marsh and placed in the center of the arena with its aperture facing a randomly chosen direction and allowed to crawl until it reached the outer edge of the test surface. The snail was then removed and the arena and collar were rotated 90°. A tracker snail was then placed next to the beginning of the marker's trail and allowed to crawl until it reached the collar. Once the tracker reached the edge of the arena, the trails of both snails were outlined and traced onto paper. Between trials the test surface was cleaned with detergent and 90% ethanol (HAMILTON, 1977b).

The length of the marker's trail (L_m), the tracker's trail (L_t), and the portion of the tracker's trail coincident with the marker's trail (L_c) were measured using a curvimeter (Figure 2). A tracker's trail had to overlap the marker's trail completely in order to be considered coincident. The degree of trail following exhibited by each tracking snail was estimated using the following Coincidence Index (C.I.) adopted from TOWNSEND (1974):

$$C.I. = L_c/(L_m \cdot L_t)^{1/2}$$
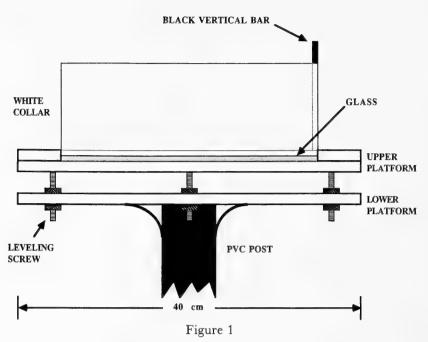
Snails that either stopped or failed to reach the edge of the arena within 5 min were excluded from the analysis. In order to estimate the degree of coincidence expected by chance, pairs of randomly selected marker trails were superimposed to serve as control values for L_m, L_t, L_c, and C.I.

The lengths of marker, tracker, and coincident trails were compared using a one-way analysis of variance (ANOVA). Coincidence Indices for treatment and control groups were analyzed via a Kruskal-Wallis one-way layout test and distribution-free multiple comparisons based on mean ranks (HOLLANDER & WOLFE, 1973).

Microscopic Examination of Trails

Microscopic comparisons of trails deposited by the same snail while crawling toward an artificial stalk (black vertical bar) and in the absence of this directional stimulus were conducted using both light (Nikon Optiphot compound scope; differential interference contrast [Nomarski]) ($n = 15$) and scanning electron microscopy (SEM) (Jeol 840-II scanning electron microscope) ($n = 10$). Because most fixation procedures destroyed trails or appeared to alter their natural structure, mucous trails deposited on glass microscope slides (40 mm × 25 mm) were either air dried (light microscopy) or frozen in liquid nitrogen (SEM) immediately after deposition. Following freezing, slides containing trail samples for SEM were critical-point dried, mounted on specimen stubs, coated with gold-palladium, and examined at 20 kV.

The elemental composition of trails of visually oriented and non-oriented marker snails ($n = 7$) were compared using energy dispersive microanalysis. Trail samples were obtained by allowing snails to crawl over carbon SEM stubs (14-mm diameter) in the presence or absence of a

Figure 1

Side view of experimental arena.

visual directional stimulus. Trails and stubs were dried in a desiccator for 1 h and coated with carbon for observation in a Cambridge S4-10 stereoscan scanning electron microscope equipped with a Tracor Northern TN 2000 microanalyzer.
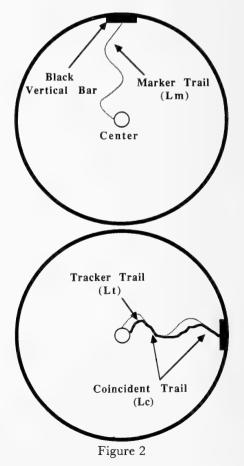
RESULTS

When placed in the arena, tracker *Littorina irrorata* detected and followed conspecifics' trails in 65% of all trials ($n = 80$). The frequency of trail following varied from 85% ($n = 20$) in trials in which the visual orientational stimulus was present for both snails to 35% ($n = 20$) in trials in which the vertical bar was present only for tracker snails. The trails of marking snails crawling in the absence of the visual stimulus (A/P or A/A) were significantly longer and more circuitous than those of snails crawling toward the vertical bar, but not significantly longer than controls ($F = 8.04$, d.f. $= 4, 95$; $P < 0.001$; Figure 3).
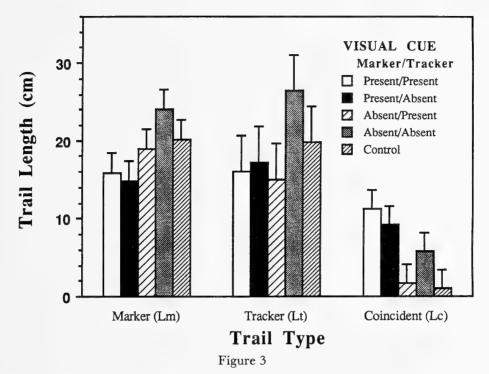
Table 1

Experimental treatments used to determine the effect of a visual orientational cue on the degree of trail following.

| Treatment | Artificial stalk | |
	Marker	Tracker
P/P	Present	Present
P/A	Present	Absent
A/P	Absent	Present
A/A	Absent	Absent
Control		

Figure 2

Typical trails deposited by marker and tracker snails crawling in either the presence or absence of a visual directional stimulus.

Figure 3

Mean marker, tracker, and coincident trail lengths and 95% comparison intervals for the four experimental treatments in which a visual directional stimulus was either present or absent for marker and tracker *Littorina irrorata*. Pairs of marker trails were randomly selected and superimposed to serve as controls.
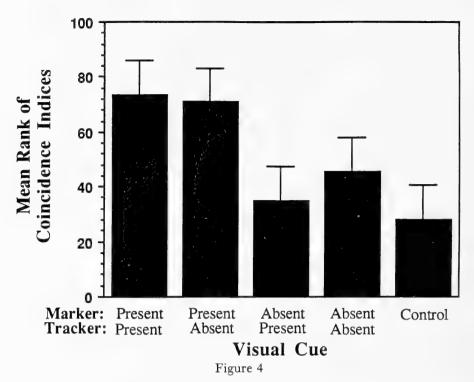
The lengths of tracker trails for the Absent/Absent (A/A) treatment were significantly longer than the tracker trails for all other treatments ($F = 15.46$, d.f. = 4, 95; $P < 0.001$; Figure 3). When coincident trails were standardized by the length of the marker and tracker trails (calculated C.I.), the degree of trail following was significantly greater under conditions in which the marker trail was laid in the presence of a visual directional stimulus ($H = 43.79$, d.f. = 4; $P < 0.001$; Figure 4). No significant differences were found between the two treatments in which the artificial stalk was present for marker snails (P/P and P/A). Similarly, the treatments in which the orientational cue was absent for marker snails (A/P and A/A) were not significantly different from each other or from the controls.

Microscopic examination of trails using either Nomarski optics or SEM revealed no noticeable differences in the overall physical and morphological structure of trails laid down by the same snail while crawling in the absence or the presence of a visual directional stimulus. Both trails were thin mucous mats of parallel threadlike structures oriented along the trail's axis (Figure 5). The strands are similar to those previously described by STIRLING & HAMILTON (1986) for stained *Littorina irrorata* trails and resemble those reported for other gastropods including *Helix aspersa* (SIMKISS & WILBUR, 1977) and the tracking mud snail *Ilyanassa obsoleta* (BRETZ & DIMOCK, 1983). A comparison of the elemental composition of air-dried marker trails using X-ray microanalysis revealed significant con-

centrations of sulfur, sodium, magnesium, potassium, chlorine, and calcium, regardless of whether they were laid down in the presence or absence of a visual stimulus. Although the relative concentrations of the elements differed slightly between samples, the overall composition of the trails and the seawater control were not significantly different.

DISCUSSION

Although trail following is an obvious component of the behavior of *Littorina irrorata,* few published studies have attempted to establish the natural conditions under which it occurs or determine its functional role. This study has demonstrated that *L. irrorata* pursues conspecific mucous trails that have been deposited in response to visual orientational cues more frequently and with greater precision (coincidence) than trails that were laid in the absence of such cues. The frequencies of trail detection and tracking not only were higher in treatments with a directional cue present for marking snails, but snails also tended to follow greater proportions of markers' trails over longer distances (Figures 3, 4). Furthermore, the presence of a directional stimulus for tracker snails (treatments A/P and P/P) did not significantly influence their responses to a conspecific's trail. These results suggest that mucous trails deposited by visually orienting marker snails contain different or more discernible information than trails deposited by snails

Figure 4

Mean ranks and 95% comparison intervals (Kruskal-Wallis one-way layout test) for the calculated coincident indices (C.I.).
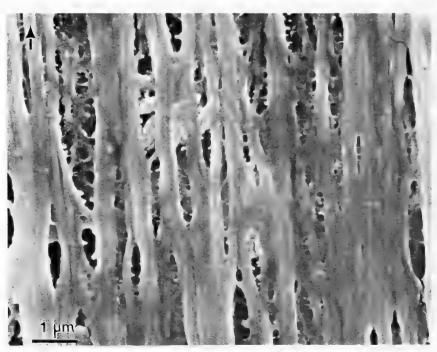
Figure 5

Scanning electron micrograph of a mucous trail deposited by *Littorina irrorata*. Arrow indicates the direction of trail deposition.

crawling in the absence of a visual directional cue. Therefore, trail following might serve as an important orientational mechanism facilitating the location of *Spartina* stalks by *Littorina* as the tide advances.

The role of mucous trails in molluscan orientation has been well documented, especially for homing gastropods. Although several proposed homing mechanisms have been extensively studied, including external cues, kinesthetic, and topographic memory (FUNKE, 1968), direct olfaction and contact chemoreception with previously deposited trails usually are considered most plausible (COOK *et al.*, 1969; COOK, 1969, 1971; COOK & COOK, 1975; COOK, 1979a, b, 1980; McFARLANE, 1980; ROLLO & WELLINGTON, 1981). COOK (1979a) proposed that homing is accomplished via a dual chemosensory mechanism in which separate pheromones are responsible for trail following and distance chemoreception. Observations of the homing behavior of several terrestrial snails and slugs support this hypothesis (ROLLO & WELLINGTON, 1981). The use of chemical trails for homing is not restricted to gastropods and has been reported for other mollusks including the chitons *Acanthozostera gemmata* (THORNE, 1968) and *Acanthopleura gemmata* (CHELAZZI *et al.*, 1987).

The heightened response of trackers to trails deposited by marker snails that had been oriented to visual cues suggests that those mucous trails possess encoded information that triggers or enhances tracking behavior. Although the mechanisms that mediate either tracking and homing behavior or the detection of trail polarity have not been determined for any gastropod, most workers hypothesize that either chemical pheromones or physical discontinuities in trails are involved (COOK *et al.*, 1969; COOK, 1971; TROTT & DIMOCK, 1978; COOK, 1979a, b; BOUSFIELD *et al.*, 1981; BRETZ & DIMOCK, 1983). Thus, one might hypothesize that structural or chemical differences exist between the trails of visually oriented versus non-oriented *Littorina irrorata*, making those trails distinguishable to a tracking snail.

Molluscan mucus, although mostly water (91–98%) (DENNY, 1983, 1984), is chemically complex and frequently contains high molecular weight glycoproteins, proteins, amino acids, carbohydrates (predominantly mucopolysaccharides) and lipids (HUNT, 1967; WILSON, 1968; TRENCH *et al.*, 1972; TRENCH, 1973; WHITEHEAD, 1978; GRENON & WALKER, 1980; DENNY, 1983). BOUSFIELD *et al.* (1981) propose that metabolic substances, including known molluscan attractants such as butyrate and propionate, might be responsible for the triggering and specificity of tracking behavior by *Biomphalaria*. Informational differences in mucous trails of the homing pulmonate *Onchidium verruculatum,* which deposits inbound trails that contain little or no directional information relative to outbound trails, also have been reported (McFARLANE, 1981). McFARLANE (1981) hypothesized that the reduction in information in the trail of *O. verruculatum* is caused by a decrease in the deposition of a specific trail substance in inbound versus outbound trails. More recently CHELAZZI

et al. (1987) suggested that the homing chiton *Acanthopleura gemmata* minimizes the chances of following a conspecific's trail by depositing a trail containing both species-specific and quasi-individual information. Regulation of the information content of mucous trails might be accomplished by independent neuronal control of chemicals secreted from different mucous cells present in the snail's pedal gland (CHASE & BOULANGER, 1978).

A less likely explanation for the tendency of tracker snails to follow trails deposited by visually orienting markers is that non-orienting markers may deposit some substance in their pedal mucus that deters trail following. When displaced from its natural habitat and disoriented, *Littorina irrorata* might secrete a chemical with its mucus that inhibits the tracking response or otherwise renders the trails unattractive to conspecifics. It is unlikely that the trail is made repellent, per se, because tracker snails readily crossed trails made by non-oriented markers, and in fact would follow short segments thereof. However, the marine opisthobranch *Navanax inermis* has been shown to secrete a bright yellow alarm pheromone into its pedal mucus when mechanically disturbed by an investigator or attacked by a potential predator (SLEEPER *et al.*, 1980). A tracking *Navanax* quickly stops trail following and deviates from such a trail. *Littorina irrorata* does exhibit an avoidance response to secondary metabolites present in some marine macroalgae (TARGETT & McCONNELL, 1982). Displaced and disoriented snails might deposit similar metabolites or substances with their mucus.

Microscopic comparison of trails laid in the presence versus the absence of a visual stimulus revealed no obvious physical, morphological, or chemical differences between the two types of trails. Although trails were composed of thin mats of threadlike strands resembling those that may be involved in determining trail polarity in *Ilyanassa obsoleta* (BRETZ & DIMOCK, 1983), neither type of trail possessed any unique morphological structures or chemical elements that were not found reciprocally. Because the microanalysis technique that was employed is limited to detection of inorganic elements only, the organic components of the mucous trails have not been examined.

As with many other species, *Littorina irrorata* most likely possesses a suite of orientational abilities integrating several sensory stimuli and orientational mechanisms, including visual, tactile, and chemical cues (ABLE, 1980). Complex orientational repertoires have been described for other shore-living animals, especially arthropods (HERRNKIND, 1972). The influence of environmental stimuli, including visual objects, on the orientation of *L. irrorata* in the marsh has been studied extensively (BINGHAM, 1972; HAMILTON, 1978b; HAMILTON & WINTER, 1982). Previously deposited mucous trails, as well as other non-visual mechanisms such as geotaxis, might augment visual information or serve as substitute reference systems when snails are deprived of visual and other stimuli, or when cues are rendered ambiguous (*e.g.,* when submerged or in darkness). Moreover, the location of vegetative areas may

be accomplished through the differential weighing of a collection of directional cues whose relative importance varies with environmental conditions and the animal's location within the marsh. Because climbing and remaining on grass stalks are critical to *L. irrorata* for avoiding high temperatures (MCBRIDE *et al.*, 1989) and predators (HAMILTON, 1976; WARREN, 1985), trail following to relocate a grass stalk or areas of vegetation has clear adaptive value. Future studies of the orientation of *L. irrorata* that involve placing a variety of directional stimuli, including visual cues and conspecific trails, in opposition with one another should provide a clearer understanding of the mechanisms influencing this snail's orientation in the marsh under different environmental conditions.

ACKNOWLEDGMENTS

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NOTES, INFORMATION & NEWS

International Commission on Zoological Nomenclature

Proposed fourth edition of the Code: The ICZN has embarked on the preparation of a new (fourth) edition of the *Code* and has established an Editorial Committee for that purpose. Publication is expected to be in late 1994 or in 1995. Many possible amendments to the *Code* have been suggested and these will be examined by the Editorial Committee. The Commission invites the submission of further possible amendments to the current (1985) *Code.*

Official lists and indexes of names and works in zoology—supplement: The *Official Lists and Indexes* was published in 1987. This gave all the names and works on which the ICZN had ruled since it was set up in 1895, up to December 1985. There were about 9900 entries. In the years since 1985, 544 names and 3 works have been added to the *Official Lists and Indexes.* A supplement has been prepared giving these additional entries, together with some amendments to entries in the 1987 volume. This supplement can be obtained without charge from the following addresses, from which the *Official Lists and Indexes* also can be ordered at the price shown:

The International Trust for Zoological Nomenclature, British Museum (Natural History), Cromwell Road, London SW7 5BD, U.K. (Price : £ 60 or $110) or

The American Association for Zoological Nomenclature, %NHB Stop 163, National Museum of Natural History, Washington, D.C. 20560, USA (Price: $110; $100 to A.A.Z.N. members).

Call for nominations for new members of the ICZN: Several members of the Commission reach the end of their terms of service at the close of the XXIV General Assembly of the International Union of Biological Sciences to be held in Amsterdam, in July 1991. The Commission now invites nominations, by any person or institution, of candidates for membership. Article 2b of the Constitution prescribes that: "The members of the Commission shall be eminent scientists, irrespective of nationality, with a distinguished record in any branch of zoology, who are known to have an interest in zoological nomenclature." ("Zoology" here includes the applied biological sciences that use zoological names.)

Nominations made since September 1987 will be reconsidered automatically and need not be repeated. Additional nominations, giving date of birth, nationality, and qualifications (by the criteria mentioned above) of each candidate should be sent by 15 June 1990 to the address below.

Applications and Opinions published in the Bulletin of Zoological Nomenclature: Comment or advice on applications is invited for publication in the *Bulletin,* and should be sent to the address below.

Applications published 29 March 1989 in Vol. 46, Part 1 of the *Bulletin:*

Case 2668—*Drepanites* Mojsisovics, 1893, and *Hyphoplites* Spath, 1922 (Mollusca: Cephalopoda): proposed conservation.

Applications published 23 June 1989 in Vol. 46, Part 2 of the *Bulletin:*

Case 2403—*Valanginites* Sayn in Kilian, 1910 (Cephalopoda: Ammonoidea): confirmation of the author of the genus, and of *Ammonites nucleus* Roemer, 1841, as its type species.
Case 2642—Polygyridae Pilsbry, 1894 (Mollusca: Gastropoda): proposed precedence over Mesodontidae Tryon, 1866.

Opinions published 29 March 1989 in Vol. 46, Part 3 of the *Bulletin:*

Opinion 1518—*Harpa articularis* Lamarck, 1822 (Mollusca: Gastropoda): specific name conserved.
Opinion 1519—*Ammonites neubergicus* Hauer, 1858 (Cephalopoda: Ammonoidea): to be given precedence over *Ammonites chrishna* Forbes, 1846.

Opinions published 23 June 1989 in Vol. 46, Part 2 of the *Bulletin:*

Opinion 1539—*Conus floridanus* Gabb, 1869 (Mollusca: Gastropoda): not to be given precedence over *Conus anabathrum* Crosse, 1865.
Opinion 1540—*Avicula gryphaeoides* J. de C. Sowerby, 1836 (Mollusca: Bivalvia): specific name conserved.

Address for comments, nominations, and applications:

Executive Secretary, I.C.Z.N.
%British Museum (Natural History)
Cromwell Road
London SW7 5BD, U.K.

BOOKS, PERIODICALS & PAMPHLETS

The Banana Slug.
A Close Look at a Giant Forest Slug
of Western North America

by ALICE BRYANT HARPER, with photographs by DANIEL
HARPER. 1988. Bay Leaves Press, 7000 Soquel Drive,
Aptos, California 95003 (in cooperation with the Santa
Cruz Museum Association). 32 pp. Price: $6.95.

Written in the style of a somewhat informal but well-
informed article in *National Geographic,* Alice Bryant Har-
per has captured the essence of the "banana slug," con-
sisting in western North America of three species of the
pulmonate genus *Ariolimax.* Her approach is that of a
serious amateur in the best sense of the phrase. The word
"amateur" comes from the Latin *amator* and the French
amare, meaning "to love." Fascination, love, and respect
for the banana slug and its role in coastal forest commu-
nities is evident. Evident too is that Ms. Harper has taken
her subject seriously. A wealth of information is presented
concisely and accurately (Drs. Barry Roth and F. G. Hoch-
berg are acknowledged for scientific advice and editorial
suggestions).

Although only 32 pages long, this booklet covers much
ground. Included topics are the slug's habitat, distribution
and range, mating behavior and reproduction, morphology,
diet, and predators, as well as the role of slime. Also
provided is a list of selected references to some popular
and more rigorously scientific sources.

The booklet is amply and superbly illustrated with color
photographs taken by the author's husband, Daniel Har-
per. Not only are the photographs beautiful, but they are
a vital part of the book, illustrating and extending the
textual information. The color plates, prepared and print-
ed by Dai Nippon Printing Company, are excellent.

The banana slug has been the subject of some consid-
erable publicity, controversy, and silliness in recent years.
It is the mascot of the University of California at Santa
Cruz, was pushed, unsuccessfully, to become the California
State mollusk, and has occasionally been the featured in-
gredient in slug recipe contests. All parties to such dis-
cussions and events would do well to read Ms. Harper's
book, from which might be gained some respect for a
fascinating creature. Information and affection go a long
way toward overcoming prejudice and fear.

D. W. Phillips

Pelagic Snails. The Biology of
Holoplanktonic Gastropod Molluscs

by CAROL M. LALLI AND RONALD W. GILMER. 1989.
Stanford University Press, Stanford, California. XIV +
259 pp. Price:$49.50.

There are an estimated 40,000 Recent species of marine
gastropod mollusks. While many of these have a planktonic
larval stage only a very few, some 140 species, have suc-
cessfully adapted to completing their entire life cycle in
the water column as holoplanktonic gastropods. It is these
mollusks that are treated by Lalli and Gilmer. Also dis-
cussed are the surface-living janthinids and glaucids.

The majority of planktonic gastropods belong to three
groups: the prosobranch heteropods and the opisthobranch
thecosomatous (shelled) and gymnosomatous (naked) ptero-
pods. The animals constitute a small fraction of plankton
samples and have until recently been available for study
primarily from bulk preserved samples. A substantial lit-
erature has accumulated on the anatomy of heteropod and
pteropod species. Some excellent work was done as much
as a century ago, but virtually all was based on preserved
material. When simply placed directly in preservative
without being relaxed, the animals frequently become dis-
torted. This has unfortunately led to erroneous conclusions
such as the description of aberrant stages in the develop-
ment of thecosomes.

In recent years the study of living planktonic mollusks
has added considerably to our knowledge of the group.
Both Lalli and Gilmer contributed substantially to the
literature containing the new findings. The book concen-
trates on the living animals with the text almost bringing
them to life. The book contains a wealth of new infor-
mation gathered by Lalli and Gilmer over a period of
years, including new descriptions of feeding and flotation
in euthecosomes. The color photographs are a superb sec-
tion of the book. For example, the photo of *Cavolina tri-
dentata* with its mantle appendages extended is something
that would never be seen in bulk preserved materials.

The book has been carefully researched, drawing on
information published in a variety of fields. By drawing
on all the available information the authors have presented
a balanced account of our current understanding of pelagic
mollusks. They have been rigorous in pointing out gaps
in our knowledge of the group and avenues open for future
research.

Pelagic Snails. The Biology of Holoplanktonic Gastropods
is an excellent book. It is must reading for not only mal-
acologists but also anyone interested in plankton.

F. E. Wells

Molluscs: Benthic Opisthobranchs
(Mollusca: Gastropoda)

by T. E. THOMPSON. 1988. 2nd edition. Synopsis of the
British Fauna, 8. E. J. Brill/Dr. W. Backhuys, Leiden,
The Netherlands. 356 pages, plus eight color plates. Soft
bound, 115 guilders (about US $57.50).

This volume is the revised and updated second edition of Thompson and Brown's *British Opisthobranch Molluscs* (1976). Designed as a field and identification guide to opisthobranch species of British waters, *Molluscs: Benthic Opisthobranchs* complements two more-detailed Thompson monographs, *Biology of Opisthobranch Molluscs, I* (1976) and *II* (1984; with G. H. Brown), published by The Ray Society. Having identified a species using the present guide, readers are advised to turn to those earlier monographs for further information.

After brief introductory accounts of the general structure, biology, collection and preservation, and classification of opisthobranchs, *Molluscs: Benthic Opisthobranchs* presents a key to the families of British opisthobranchs. The key, based on external features, applies only to families represented by British species, and excludes pteropods and pyramidellids.

The bulk of the book (315 of 356 pages) is a systematic and descriptive account of the opisthobranch species of British waters. Of the approximately 3000 species of opisthobranchs worldwide, about 5% have been reported from the shallow waters around the British Isles. For each family, a key to genera and species, again based largely on features that can be discerned without dissection, is presented. Each informative species account includes a list of best known synonyms, a description, a set of drawings (generous external views, some with inserts to show details), and notes on biology and distribution. Information on known distribution emphasizes localities around the British Isles, and Thompson cautions that the distribution list should not be regarded as complete. Even so, several species that are described and illustrated in this volume occur on the Pacific, Atlantic, or both coasts of North America.

A notable addition to this new edition is a section of eight excellent color plates illustrating 32 of the described species.

Molluscs: Benthic Opisthobranchs is a fine field guide to British opisthobranchs written by a knowledgeable and skilled author. The book is informative, well written, and well illustrated. The decision whether or not to purchase the volume will likely depend on geography and individual circumstances. For a European malacologist working with field collections, the answer is likely to be yes. For a North American not likely to collect opisthobranchs from British waters, the answer may still be yes, perhaps depending on whether the more comprehensive Thompson volumes, *Biology of Opisthobranch Molluscs, I, II,* are already on the book shelf.

D. W. Phillips

Cephalopods Past and Present

edited by JOST WIEDMANN AND JURGEN KULLMAN. 1988. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, West Germany. 756 pages, 375 figures, 16 plates. Paper, DM 198 (US $124.00).

The symposium volume *Cephalopods Past and Present* contains 57 papers on various aspects of the paleontology and biology of cephalopods. The symposium was held in Tübingen (1985) and attracted participants from around the world; nevertheless, all but four of the papers are in English.

Like most symposium volumes, this one promises somewhat more than it delivers and has flaws (or at least shortcomings) that probably are intrinsic to the symposium format. Despite a title implying a wide-ranging approach to cephalopods, past and present, topical coverage is highly uneven, as are the papers as a group. Individual contributions vary in length from 4 to over 20 pages and in content from literature reviews to presentations of new research data. Publication three years after the symposium means that some papers are already out of date.

Readers expecting from the title to find a rich sample of papers on living cephalopods are likely to be disappointed. Nevertheless, scattered among the vast majority of papers concerning past cephalopods are several of interest to students of present ones. Among these are contributions by Packard ("Visual tactics and evolutionary strategies"), Boletzky ("Characteristics of cephalopod embryogenesis"), Arnold ("Some observations on the cicatrix of *Nautilus* embryos"), Jefferts ("Zoogeography of northeastern Pacific cephalopods"), and Nixon ("The feeding mechanisms and diets of cephalopods—living and fossil"). Although this symposium, in honor of the late Professor Schindwolf, was to encourage the collaboration of zoologists and paleontologists, few papers served as bridges. A notable exception was a contribution by Reyment ("A foraging model for shelled cephalopods") who used data on living *Nautilus* to test the relevance of a foraging model for fossil cephalopods.

Students of living cephalopods may find the $124 price tag too dear for the relatively scant harvest, but paleontologists will be more richly rewarded. Hopefully, libraries will purchase this volume so that readers can follow their interests selectively.

D. W. Phillips

Sea of Cortez Marine Invertebrates: A Guide for the Pacific Coast, Mexico to Ecuador

by ALEX KERSTITCH. 1989. Sea Challengers, 4 Somerset Rise, Monterey, CA 93940. 114 pages, including 283 color photographs. Paperback, $21.50 (plus 6% sales tax for California residents and $2.35 shipping).

Alex Kerstitch's *Sea of Cortez Marine Invertebrates* continues the Sea Challengers tradition of producing magnificently illustrated guides to marine fauna.

Color plates of 283 invertebrate species occurring in the

Gulf of California are presented. These include 110 species of mollusks. Most of the exquisite photographs illuminate subjects in their natural habitats, yet most are sufficiently detailed and informative to allow unambiguous identification of the species. An adjacent text lists diagnostic features that identify positively each animal and separate them from closely related species.

For each animal the accompanying text includes the diagnostic description, a size range, the typical habitat (including bathymetric range), geographical distribution, and a set of remarks on natural history, as permitted by available knowledge and space on the page. Unfortunately, little is known about the natural history of most Gulf invertebrates.

In addition to the species accounts, the book includes a foreword by R. C. Brusca that introduces readers to the modern history and ecology of the Gulf of California, a glossary, capsule descriptions of and a pictorial key to the represented major phyla, and a reference list.

Some readers will find occasional sources of minor annoyance—usage of "shells" for live mollusks, Pelecypoda instead of Bivalvia, and invented "common" names. Because the majority of marine invertebrates from the Gulf do not have accepted common names, the author has invented new ones to fill a perceived void. In many cases the designated vernacular name refers to a notable attribute of the animal, but in others the name is so general (clawed shrimp) or so parochial as perhaps to be counterproductive—someone familiar with the central California marine fauna will find that, for instance, the names clown nudibranch, blue-spotted hermit crab, and purple sea urchin are applied to different species in the Gulf. Such quibbles are minor, however, compared with the many excellent features of this guide book.

Kerstitch has admirably succeeded in reaching his twin goals: to allow quick and accurate identification of common Gulf invertebrates from photographs and to whet the reader's appetite to learn more about the marine fauna of the Gulf of California. The book is useful, informative, and beautiful, and belongs on the shelf of every Pacific coast marine biologist.

D. W. Phillips

Cowries and Their Relatives of Southern Africa. A Study of the Southern African Cypraeacean and Velutinacean Gastropod Fauna

by WILLIAM R. LILTVED. 1989. Verhoef, Seacomber Publ.: Capetown, South Africa. 208 pages; 298 + 8 figs. The book may be obtained from Mal de Mer Enterprises, P.O. Box 482, West Hempstead, NY 11552. Hardbound, $65.00 plus postage ($4 in USA, $7 overseas).

These two gastropod superfamilies have undergone a remarkable radiation in southern Africa, and here is a book that has done them justice. The book discusses in

detail the endemic species of *Cypraea* but not most of the non-endemic taxa. However, all of the Ovulidae and Triviidae are covered. Color illustrations are used throughout, including pictures of living animals in most cases, and several views to show variation in morphology and color pattern. Both shells and animals are described, notes are provided on natural history, and maps show distributions. Introductory materials discuss the morphology, anatomy, development, ecology, and evolution of these families; included are some outstanding anatomical line drawings.

This book is recommended for anyone interested in these fascinating marine gastropods.

Gene Coan

Two Books on Japanese Marine Mollusks

Gastropods from Continental Shelf and Slope around Japan (25 March 1988; 203 pp) and Bivalves from Continental Shelf and Slope around Japan (22 March 1989; 190 pp)

by T. OKUTANI, M. TAGAWA & H. HORIKAWA. Japan Fisheries Resource Conservation Association, Tokyo Suisan Bldg., 6th Floor, Toyomi-cho 4-18, Chuo-ku, Tokyo 104, Japan.

These two volumes cover species obtained during a special program called "The Intensive Research of Underexploited Fisheries Resources on Continental Slopes," conducted from 1977 to 1979. The gastropod volume illustrates and describes 160 taxa, including one new species, *Buccinum koshikianum* Okutani. The bivalve book also features 160 taxa, including one new venerid, *Phacosoma nipponicum* Okutani & Habe. Each species covered has a description in Japanese and in English, but no synonymy. The most impressive feature of these two volumes is the quality of the color photographs of the specimens.

Gene Coan

New Printing of Light's Manual: Intertidal Invertebrates of the Central California Coast

edited by R. I. SMITH & J. T. CARLTON. 3rd edition 1975 (4th printing 1989). University of California Press, 2120 Berkeley Way, Berkeley, CA 94720. $40.00, although discounts of 20% are widely available.

The third edition of *Light's Manual,* first issued in 1975, is now appearing as a fourth printing, 1989. The fourth printing contains a number of minor textual changes, corrections, and new names, plus three pages of addenda. However, some groups, notably polychaetes, amphipods, and nudibranchs, have been so extensively reworked over

the past decade that it has proved impossible to provide complete errata and addenda. For owners of the third printing (1980), a set of changes entered in the fourth printing is available, gratis, from R. I. Smith, Department of Integrative Biology, University of California, Berkeley, CA 94720.

Sincere thanks are again due Dr. Smith for this con-tinuing generosity in making such updates possible. How-ever, the time would seem to have come, indeed long ago, for the University of California Press to speed production of a fully revised fourth edition. The cover of my 1975 volume, so full of sheets containing errata and addenda, will no longer close.

Information for Contributors

Manuscripts

Manuscripts must be typed on white paper, 8½″ by 11″, and double-spaced throughout (including references, figure legends, footnotes, and tables). If computer generated copy is to be submitted, margins should be ragged right (*i.e., not* justified). To facilitate the review process, manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics. Metric and Celsius units are to be used.

The sequence of manuscript components should be as follows in most cases: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, figures, footnotes, and tables. The title page should be on a separate sheet and should include the title, author's name, and address. The abstract should describe in the briefest possible way (normally less than 200 words) the scope, main results, and conclusions of the paper.

Literature cited

References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Smith, 1951), for two authors (Smith & Jones, 1952), and for more than two (Smith *et al.,* 1953).

The "literature cited" section must include all (but not additional) references quoted in the text. References should be listed in alphabetical order and typed on sheets separate from the text. Each citation must be complete and in the following form:

a) Periodicals

Cate, J. M. 1962. On the identifications of five Pacific *Mitra.* Veliger 4:132–134.

b) Books

Yonge, C. M. & T. E. Thompson. 1976. Living marine molluscs. Collins: London. 288 pp.

c) Composite works

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117–135. *In:* R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal invertebrates of California. Stanford Univ. Press: Stanford, Calif.

Tables

Tables must be numbered and each typed on a separate sheet. Each table should be headed by a brief legend.

Figures and plates

Figures must be carefully prepared and should be submitted ready for publication. Each should have a short legend, listed on a sheet following the literature cited.

Text figures should be in black ink and completely lettered. Keep in mind page format and column size when designing figures.

Photographs for half-tone plates must be of good quality. They should be trimmed off squarely, arranged into plates, and mounted on suitable drawing board. Where necessary, a scale should be put on the actual figure. Preferably, photographs should be in the desired final size.

It is the author's responsibility that lettering is legible after final reduction (if any) and that lettering size is appropriate to the figure. Charges will be made for necessary alterations.

Processing of manuscripts

Upon receipt each manuscript is critically evaluated by at least two referees. Based on these evaluations the editor decides on acceptance or rejection. Acceptable manuscripts are returned to the author for consideration of comments and criticisms, and a finalized manuscript is sent to press. The author will receive from the printer two sets of proofs, which should be corrected carefully for printing errors. At this stage, stylistic changes are no longer appropriate, and changes other than the correction of printing errors will be charged to the author at cost. One set of corrected proofs should be returned to the editor.

An order form for the purchase of reprints will accompany proofs. If reprints are desired, they are to be ordered directly from the printer.

Send manuscripts, proofs, and correspondence regarding editorial matters to: Dr. David W. Phillips, Editor, 2410 Oakenshield Road, Davis, CA 95616 USA.

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CONTENTS — *Continued*

Allozyme Variation in the Australian Camaenid Land Snail *Cristilabrum primum*: A Prolegomenon for a Molecular Phylogeny of an Extraordinary Radiation in an Isolated Habitat

by

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Abstract.   A group of 27 species of land snails belonging to three genera have been discovered isolated in the 52-km long limestone Ningbing Range in northwest Australia. These endemic species have very restricted geographic ranges (averaging 1 km²) and are typically allopatric. As the three genera have no known close relatives, it is assumed that the taxa evolved *in situ* since camaenids colonized Australia in the Miocene. We studied genetic variation in one species and compared it with two congeners and representatives of the other two genera to provide a basis for the development of a molecular phylogeny of this remarkable radiation. Electrophoretically detected variation at 21 allozyme loci in *Cristilabrum primum* is described; this species is shown to be highly variable ($P = 0.71$, $\bar{H} = 0.22$) and outcrossing. Multilocus differentiation within *C. primum* is small (Nei's genetic distance, $D = 0$–0.02) and typical of conspecific populations. Preliminary data show *C. primum* is weakly differentiated from one parapatric neighbor (*C. grossum*: $D = 0.04$) and well-differentiated from the other (*C. monodon*: $D = 0.17$); all three species are, however, well differentiated anatomically and conchologically. The genetic distances between *Cristilabrum* and the other two genera (*Turgenitubulus*, $\bar{D} = 0.27$; *Ningbingia*, $\bar{D} = 0.50$) are larger and bode well for the development of an allozyme-based phylogeny.

INTRODUCTION

An extraordinary radiation of camaenid land snails has been discovered in an isolated series of limestone hills in the northeast corner of Western Australia. Twenty-nine endemic species of pulmonates have been described from a narrow 52-km long chain of isolated limestone hillocks, the Ningbing Range and adjacent Jeremiah Hills (SOLEM, 1981, 1985, 1988a, b, 1989a, b). These species are mainly allopatric in distribution and the 27 species of camaenids are remarkable for their very restricted geographic ranges,

typically less than 1 km². They occupy all available habitat in these hills, the low remnants of a Devonian reef, but cannot live on the surrounding alluvial plain and are not found in nearby sandstone ranges. The various species are well characterized on the basis of anatomical and conchological features and all but one are placed in three restricted endemic genera. The exception, *Ordtrachia elegans* Solem, 1988, belongs to a distantly related East Kimberley genus. The other three genera have not been found elsewhere, and it appears that their 26 species evolved *in*
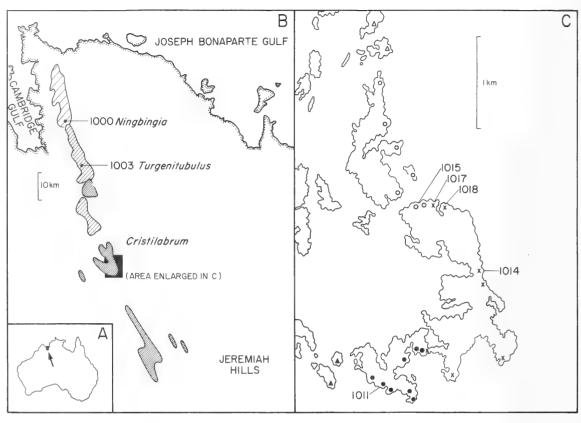
Figure 1

Locality map. A. Position of the Ningbing Range. B. Diagram showing the geographic distribution of *Ningbingia*, *Turgenitubulus,* and *Cristilabrum* in the Ningbing Range and Jeremiah Hills. Collection sites of numbered samples and generic ranges are shown. C. Enlargement of the central portion of the range of *Cristilabrum* showing position of samples relative to the main limestone outcrops: *C. primum* (×), *C. monodon* (O), *C. grossum* (●), other *C.* sp. (△▲). Source: SOLEM, 1988b.

situ since camaenids first gained access to Australia from Asia during the Miocene (SOLEM, 1988a, b). The Ningbing radiation occurs in "a little world within itself," to recall DARWIN's (1839:454) phrase, and its phylogenetic analysis begs attention and comparison with other better known examples of evolution in isolated microcosms. In this paper, we describe the genetic variation in one species as a prolegomenon to preparation of a molecular phylogeny of the radiation as a whole.

The Ningbing Range and Jeremiah Hills are located on the east fringe of the Kimberley Region, 50–100 km north of Kununurra, Western Australia (Figure 1A). The three endemic camaenid genera are allopatric, with *Ningbingia* in the North Ningbing Range, *Turgenitubulus* in the Central Ningbing Range and adjacent hills, and *Cristilabrum* in the south portion of the Central Ningbing Range, South Ningbing Range, and adjacent Jeremiah Hills (Figure 1B). With many isolated hills yet to be explored, 27 endemic species are now recognized: *Ningbingia* Solem, 1981, with six species and one subspecies; *Turgenitubulus* Solem, 1981, with eight species; and *Cris-*

tilabrum Solem, 1981, with 13 species (12 described). The species' geographic ranges have been described by SOLEM (1988b); they are all continuous and discrete rather than interspersed. The median areas for species geographic ranges within genera are *Ningbingia* 1.05 km², *Turgenitubulus* 1.66 km², and *Cristilabrum* 0.63 km². There are seven cases of "same rock" microsympatry involving two species (and one involving three species). Sympatric taxa are typically characterized by marked differences in the terminal genitalia and easily observed shell differences. Undoubtedly, additional species remain to be discovered.

The Ningbing radiation occurs in a remote area of difficult access. Field work is impossible during the wet season associated with the monsoon (November through March). Some biological observations have been made early (May–June) and at the end of the dry season (November) when the snails are found estivating (SOLEM & CHRISTENSEN, 1984). All the endemic camaenids are "free sealers" and are found lying loose in limestone rubble with a sheet of calcified mucus closing the shell aperture. During the 7–8 month dry season they are inactive and depend on stored

food for survival. The snails first function as males at the beginning of their third wet season; in their fourth and subsequent wet seasons they are outcrossing hermaphrodites. Mating has not been observed, but in other probably related camaenids it is reciprocal. Longevity is unknown, but observations of other Kimberley camaenids suggest 10–15 yr is not unreasonable. The snails are highly clumped in their dispersion in the dry season; SOLEM (1988b) discusses the highly fragmented pattern of dry season distribution and the extremely small volumes (<1 m^3) occupied by some successful colonies. Although quantitative data are lacking, we get the impression that many estivation sites shelter closer to 100 than 1000 snails. A metapopulation model, made up of many small to very small subpopulations, seems appropriate to today's Ningbing endemics.

In the absence of a fossil record, the phylogeny of the Ningbing radiation must be deduced from a study of the living forms. Four independent data sets (based on shell morphology, genital anatomy, biogeography, and allozymes) provide excellent data for the preparation of hypothetical phylogenies. Observations of feeding, excretory, muscle, digestive, and nervous systems showed uniform patterns and thus could not be utilized. In order to set the stage for the subsequent development of an allozyme-based phylogeny, we measured intraspecific variation in one species, *Cristilabrum primum* Solem (1981), which is common within a restricted area (1.2 km^2) in the South Ningbing Ranges (SOLEM, 1988b). It occupies the central part of a 3.5-km long hill and is flanked to the northwest and southeast by *C. monodon* Solem (1985) and *C. grossum* Solem (1981), respectively (Figure 1C). These three species are the only members of this radiation on this particular hill and their ranges are allopatric and presently separated from one another by 100-m wide areas lacking suitable habitats. Consistent shell and anatomical differences between these three species have been described elsewhere (SOLEM, 1981, 1985) and are summarized in Table 4. To test the resolving power of an allozyme-based phylogeny, we compared *C. primum* with its two congeneric neighbors and to one representative of each of the other two endemic genera: *Ningbingia australis australis* Solem (1981), and *Turgenitubulus tanmurranus* Solem (1985). This is the first report of genetic variation in the Australian camaenid land snails so the choice of *C. primum* seems appropriate.

MATERIALS AND METHODS

All snails were collected in late May 1984 by Alan Solem, Field Associate Laurie Price, or a student assistant, K. C. Emberton. At that time of year, the snails were two months into the 6–8 month dry season and all were found estivating. Typically, the sample was collected from about 1 m^3 of rock rubble or from crevices in an area of less than 3 m^2 of limestone. Live individuals of *Cristilabrum primum* were collected at three stations, WA-1017 and WA-1018

Table 1

Presumptive loci and electrophoretic conditions for camaenids

Allozyme	Gene symbol	E.C. No.	Buffer*
Esterase 1	*Es-1*	3.1.1.1	TC 6.0
Glucose-6-phosphate dehydrogenase	*G6pd*	1.1.1.49	TBE 9/8
Glucose phosphate isomerase	*Gpi*	5.3.1.9	TC 6.0
Glutamic-oxaloacetic transaminase soluble	*Got-1*	2.6.1.1	TC 6.8
Glutamic-oxaloacetic transaminase mitochondrial	*Got-2*	2.6.1.1	TC 6.8
Glyceraldehyde-3-phosphate dehydrogenase	*Gapd*	1.2.1.12	TC 6.8
Glycerol-3-phosphate dehydrogenase	*Gpd*	1.1.1.8	TBE 9/8
Isocitrate dehydrogenase, soluble	*Idh-1*	1.1.1.42	TC 6.8
Isocitrate dehydrogenase, mitochondrial	*Idh-2*	1.1.1.42	TC 6.8
Lactate dehydrogenase	*Ldh*	1.1.1.27	TBE 9/8
Malate dehydrogenase, soluble	*Mdh-1*	1.1.1.37	TC 6.0
Malate dehydrogenase, mitochondrial	*Mdh-2*	1.1.1.37	TC 6.0
Malic enzyme cytoplasmic	*Me*	1.1.1.40	TBE 9/8
Mannose phosphate isomerase	*Mpi*	5.3.1.8	TC 6.0
Peptidase 1 (leucineamino)	*Pep-1*	3.4.11/13	TBE 9/8
Peptidase 2 (L-leucyl-L-alanine)	*Pep-2*	3.4.11/13	TBE 9/8
Peptidase 3 (leucyl glycyl glycine)	*Pep-3*	3.4.11/13	TBE 9/8
Phosphoglucomutase 1	*Pgm-1*	2.7.5.1	TBE 9/8
Phosphoglucomutase 2	*Pgm-2*	2.7.5.1	TBE 9/8
Phosphogluconate dehydrogenase	*Pgd*	1.1.1.43	TC 6.8
Sorbitol dehydrogenase	*Sord*	1.1.1.14	TBE 9/8

* *TBE 9/8.* 0.087 M Tris, 0.086 M borate, 0.001 M EDTA, pH 9.0; diluted 1:3 for gels. 0.5 M Tris, 0.065 M borate, 0.02 M EDTA, pH 8.0; undiluted for electrodes (17 hr 50 V).

TC 6.0. 0.378 M Tris, 0.165 M citrate, pH 6.0; 13.5 ml diluted to 400 ml for gel and undiluted for electrodes (18 hr 70 V).

TC 6.8. 0.188 M Tris, 0.065 M citrate, pH 6.8; diluted 1:9 for gels and 1:5 for electrodes (18 hr 50 V).

at the north end and WA-1014 in the middle of the species range (Figure 1C). These and other collection stations are mapped and described by SOLEM (1981, 1988b). *Cristilabrum primum* has a total linear range of about 1.2 km; stations WA-1017 and WA-1018 are about 50 m apart across a gully and about 0.9 km north of WA-1014. *Cristilabrum monodon* occurs immediately northwest of *C. primum* and was sampled at WA-1015, only 200 m west of WA-1017. *Cristilabrum grossum* replaces *C. primum* to the southwest on the same rock mass and was sampled at WA-1011 about 1.6 km southwest of WA-1014. The eight

species of the genus *Turgenitubulus* replace *Cristilabrum* to the north; we describe here the variation in *T. tanmurranus* from about 18 km north of *C. primum* at WA-1003. Further north again are six species of *Ningbingia* represented here by *N. australis* from WA-1000, about 31 km north of *C. primum.*

Tissues for allozyme analysis were prepared on the day of collection. Snails were quickly activated by short exposure to wet paper towels and the posterior portion of the cephalopodal mass was amputated with a razor and stored individually in cryogenic vials in liquid nitrogen. For electrophoresis in 1986–1987, the individual tissue samples were thawed and quickly minced in 0.1 mL of cold grinding solution (0.01 M Tris, 0.001 M EDTA, 0.05 mM NADP, pH 7.0) with mounted needles and a glass rod. Each homogenate was centrifuged at 10,000 g for 2 min and the supernatant was absorbed onto 3 × 9 mm paper wicks cut from Whatman No. 3 chromatography paper. The wicks were inserted into 12% horizontal gels made of Sigma starch (Sigma Chemical Co., St. Louis, MO). Electrophoretic conditions for the 21 allozymes reported here are described in Table 1. Four or five slices were cut from each gel after 17–18 hr of electrophoresis and each slice was stained for a specific enzyme following standard methods (Harris & Hopkinson, 1978; Richardson *et al.*, 1986). The esterase substrate was alphanaphthyl acetate. Three peptidases were studied: leucine aminopeptidase, L-leucyl-L-alanine peptidase and leucylglycyl-glycine peptidase. Snails from different samples were run on each gel to facilitate comparisons and a bromophenol blue dye was used to track the front. Isozymes were numbered and allozymes were assigned superscript letters a, b, *etc.*, in order of decreasing anodal mobility. Relative mobilities of all electromorphs were determined by measurement and all gels were photographed immediately after patterns were resolved. Each allozyme is identified in Table 1 by its International Union for Pure and Applied Chemistry and International Union for Biochemistry Enzyme Commission (E.C.) number. Enzyme abbreviations (gene symbols) conform to human gene nomenclature (Roychoudhury & Nei, 1988) and are typeset in capital letters to indicate the protein and in lowercase italics to indicate the presumed allele.

Multilocus genotype data for all individuals were entered into a computer and a series of statistical analyses was performed with the BIOSYS-1 computer program (Swofford & Selander, 1981). For each sample the number of alleles per locus (A), the proportion of loci polymorphic (P), and the mean individual heterozygosity ($\bar{H}$) were determined. A locus was considered polymorphic if more than one allele was detected; $\bar{H}$ was determined by direct count. Genotype frequencies at each polymorphic loci were tested for their agreement with Hardy-Weinberg expectations for a panmictic population by χ^2-test (with Levene's [1949] correction for small sample size) where appropriate and by the Fisher exact test. Intra- and in-

terpopulation genetic structuring was examined using Wright's (1978) hierarchical F-statistics (F_{is}, F_{it} and F_{st}) calculated for each locus and each sample. Intersample differentiation was estimated using the unbiased genetic distance coefficients (D) of Nei (1978) and the modified Rogers' distance coefficient (Wright, 1978). A phenogram was constructed using the UPGMA clustering algorithm (Sneath & Sokal, 1973) based on Nei's D. In addition, optimized unrooted and rooted trees were constructed by the Distance Wagner method based on the modified Rogers' distance.

RESULTS

Looking first at the large sample ($\bar{N} = 51$) of *Cristilabrum primum* from site WA-1018, we note that this population is highly variable at the 21 loci examined: 15 of the 18 loci found to be variable in the five species studied were polymorphic in *C. primum* ($\bar{P} = 0.71$). A similar high value was obtained for the variable proportion of each individual's genome, $\bar{H} = 0.22$. Comparably relatively high values for P and H were observed in the other two samples of this species; the slightly lower absolute values for samples WA-1017 and WA-1014 are attributable to smaller sample sizes (Table 2).

Relatively high levels of polymorphism and individual heterozygosity were also observed in the congeneric samples of *Cristilabrum monodon* and *C. grossum*. Excluding the small sample WA-1017, we note that for *Cristilabrum* $\bar{P} = 0.63$ (0.57–0.71) and $\bar{H} = 0.19$ (0.15–0.22). Slightly less variation was observed in *Turgenitubulus tanmurranus*: $P = 0.48$, $\bar{H} = 0.17$. In contrast, *Ningbingia australis* is only about one-third as variable: $P = 0.19$, $\bar{H} = 0.08$.

Thirty-three alleles were segregating at the 15 polymorphic loci detected in sample WA-1018 of *Cristilabrum primum*. In all 15 cases, chi-square tests of genotype frequencies provided no significant evidence for significant departure from random mating expectations ($p \geq 0.10$). The same conclusion was reached using the more appropriate Fisher exact probability tests, and with the two smaller conspecific samples of *C. primum* and the samples of *C. grossum* (12 tests) and *Ningbingia australis* (4 tests). Similarly, departures from panmictic expectations in 3 of 13 chi-square tests involving *C. monodon* and 1 of 10 tests involving *Turgenitubulus tanmurranus* proved insignificant when Fisher's exact test was applied. We conclude that these hermaphrodites have population structures involving random mating and insignificant inbreeding. This conclusion is supported by the observation of an overall $F_{is} = 0.049$, a value not significantly different from zero. In contrast, the overall $F_{st} = 0.45$ indicates significant intersample heterogeneity.

Two measures of intersample genetic divergence are shown in Table 3. Between the three samples of *Cristilabrum primum*, Nei's unbiased genetic distance was $\bar{D} = 0.010$ (range: 0.00–0.016). *Cristilabrum primum* was found

Table 2

Allele frequencies for 18 polymorphic loci in 7 samples of camaenids (*Ningbingia, Turgenitubulus, Cristilabrum*) from the Ningbing Range with summary statistics of genetic variability.*

Locus/ allele		*N. australis* 1000	*T. tanmurranus* 1003	*C. monodon* 1015	*C. primum* 1017	*C. primum* 1018	*C. primum* 1014	*C. grossum* 1011
Es-1								
	n	16	12	13	5	51	10	16
	a	—	—	0.54	0.80	0.38	0.60	0.16
	b	1.00	0.12	0.35	0.20	0.62	0.40	0.84
	c	—	0.71	0.11	—	—	—	—
	d	—	0.17	—	—	—	—	—
Gpi								
	n	14	12	13	5	56	11	16
	a	—	0.08	—	0.20	0.07	0.05	—
	b	1.00	0.63	1.00	0.60	0.75	0.77	0.69
	c	—	0.29	—	0.20	0.18	0.18	0.31
Got-1								
	n	16	12	13	5	54	11	16
	a	—	1.00	0.88	1.00	1.00	1.00	1.00
	b	—	—	0.12	—	—	—	—
	c	1.00	—	—	—	—	—	—
Gpd								
	n	13	12	13	5	44	8	13
	a	—	1.00	—	—	—	—	—
	b	1.00	—	0.15	1.00	1.00	0.88	1.00
	c	—	—	0.85	—	—	0.12	—
Idh-1								
	n	16	12	13	5	56	9	16
	a	1.00	1.00	1.00	0.60	0.75	0.78	1.00
	b	—	—	—	0.40	0.25	0.22	—
Idh-2								
	n	13	12	13	3	39	9	12
	a	1.00	1.00	1.00	0.67	0.76	0.83	0.79
	b	—	—	—	0.33	0.24	0.17	0.21
Ldh								
	n	16	12	13	5	26	10	13
	a	1.00	—	—	—	—	—	—
	b	—	0.54	0.58	1.00	0.77	1.00	0.69
	c	—	0.46	0.42	—	0.23	—	—
	d	—	—	—	—	—	—	0.31
Mdh-1								
	n	16	12	10	5	56	11	15
	a	—	—	—	0.30	0.02	0.05	—
	b	1.00	1.00	1.00	0.70	0.96	0.91	1.00
	c	—	—	—	—	0.02	0.04	—
Mdh-2								
	n	16	12	10	5	56	11	14
	a	1.00	1.00	0.85	1.00	1.00	1.00	1.00
	b	—	—	0.15	—	—	—	—
Me								
	n	14	12	13	4	56	11	16
	a	1.00	—	—	—	—	—	—
	b	—	0.46	0.42	0.62	0.54	0.46	0.47
	c	—	0.54	0.58	0.38	0.46	0.54	0.53

Table 2

Continued.

Locus/ allele	N. australis 1000	T. tanmurranus 1003	C. monodon 1015	C. primum			C. grossum 1011
				1017	1018	1014	
Mpi							
n	16	12	13	4	56	11	13
a	—	—	0.04	0.50	0.56	0.55	0.15
b	1.00	1.00	0.96	0.50	0.44	0.45	0.85
Pep-1							
n	11	12	13	5	56	11	12
a	—	0.42	—	—	—	—	—
b	—	0.58	0.04	0.90	0.72	0.82	0.71
c	0.55	—	0.96	0.10	0.28	0.18	0.29
d	0.45	—	—	—	—	—	—
Pep-2							
n	11	12	13	5	55	11	16
a	0.41	0.17	0.08	—	0.07	—	0.28
b	0.59	0.83	0.88	1.00	0.88	0.95	0.72
c	—	—	0.04	—	0.05	0.05	—
Pep-3							
n	14	12	13	5	54	11	16
a	—	0.12	—	—	—	—	—
b	—	0.42	0.96	0.60	0.48	0.77	0.37
c	—	0.46	0.04	0.40	0.52	0.23	0.63
d	1.00	—	—	—	—	—	—
Pgm-1							
n	14	12	13	5	56	11	16
a	1.00	0.04	—	—	—	—	—
b	—	0.96	0.81	—	0.26	—	—
c	—	—	0.19	1.00	0.74	1.00	1.00
Pgm-2							
n	13	12	13	5	53	11	15
a	—	0.62	0.31	0.40	0.18	0.09	0.23
b	0.62	0.25	—	—	—	—	—
c	—	0.13	0.69	0.60	0.82	0.91	0.77
d	0.38	—	—	—	—	—	—
Pgd							
n	14	12	13	4	42	9	11
a	1.00	1.00	1.00	0.75	0.98	0.78	0.91
b	—	—	—	0.25	0.02	0.22	0.09
Sord							
n	16	12	13	5	53	11	13
a	0.03	0.08	—	—	—	—	0.08
b	0.97	0.92	—	—	0.01	—	0.08
c	—	—	0.85	1.00	0.99	1.00	0.84
d	—	—	0.15	—	—	—	—
$\bar{n}$	14.2	12.0	12.6	4.8	51.3	10.4	14.4
$\bar{A}$	1.2	1.7	1.7	1.6	1.9	1.7	1.6
P	0.19	0.48	0.62	0.52	0.71	0.62	0.57
$\bar{H}$	0.08	0.17	0.15	0.24	0.22	0.19	0.19

* $\bar{n}$, mean sample size per locus; $\bar{A}$, mean no. of alleles per locus; P, proportion of polymorphic loci (monomorphic loci: *G6pd*, *Got-2* and *Gapd* excluded from this table); $\bar{H}$, mean individual heterozygosity.

Table 3

Matrix of genetic distance coefficients for species of *Ningbingia*, *Turgenitubulus*, and *Cristilabrum*. Below diagonal: modified Rogers' distance. Above diagonal: Nei's unbiased genetic distance.

Population	1	2	3	4	5	6	7
1. *N. australis*	****	0.458	0.471	0.591	0.477	0.543	0.414
2. *T. tanmurranus*	0.569	****	0.212	0.314	0.264	0.310	0.257
3. *C. monodon*	0.577	0.402	****	0.199	0.145	0.151	0.168
4. *C. primum* 1017	0.626	0.476	0.399	****	0.016	0.000	0.051
5. *C. primum* 1018	0.571	0.432	0.334	0.167	****	0.013	0.026
6. *C. primum* 1014	0.607	0.470	0.349	0.132	0.129	****	0.039
7. *C. grossum*	0.545	0.433	0.363	0.238	0.157	0.198	****

to be very similar to *C. grossum* ($\bar{D} = 0.039$, range: 0.026–0.051) but *C. monodon* was almost four times as well differentiated ($\bar{D} = 0.165$, range: 0.015–0.20). In contrast, the intergeneric genetic distances were much greater:

Cristilabrum–Turgenitubulus $\bar{D} = 0.27$ (0.21–0.31)
Cristilabrum–Ningbingia $\bar{D} = 0.50$ (0.41–0.59)

These distance data were clustered using the UPGMA algorithm to produce a phenetic tree with a cophenetic correlation of 0.979 (Figure 2A). A phenogram based on modified Rogers' distances and the Distance Wagner procedure, with *N. australis* as the outgroup for purposes of rooting, was found after optimization to have a total length of 1.195 and a cophenetic correlation of 0.997 (Figure 2B).
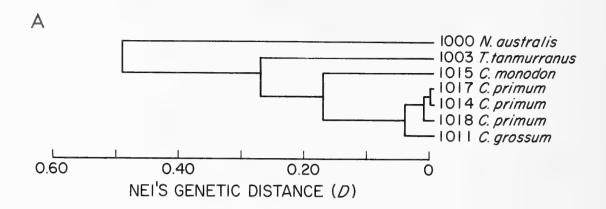
DISCUSSION
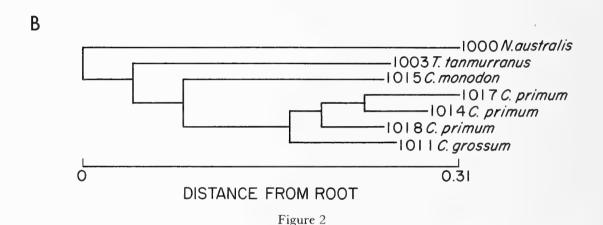
In this first study of genetic variability in Australian camaenids, we have sought to establish whether these pulmonates are variable enough for their allozymes to be useful in population studies. Second, we needed to establish whether the morphologically defined species are sufficiently well differentiated from one another for allozymic variation to be used to construct phylogenetic trees. Studies of more than 20 loci in a large sample of *Cristilabrum primum* and relatives shows that both questions can be answered affirmatively. *Cristilabrum primum* is both variable and outcrossing (amphimictic) and the study of allozymic variation promises to lead to a phylogenetic hypothesis for the radiation as a whole. Although the samples representative of the other four species are small ($\bar{N} = 13.3$) they are adequate to estimate both P, $\bar{H}$, and D as 21 loci were examined (GORMAN & RENZI, 1979; NEI, 1987).

We have found that *Cristilabrum primum* ($P = 0.62$–0.71, $\bar{H} = 0.19$–0.22) is more variable than average for mollusks; NEVO *et al.* (1984) summarized published data for 46 species finding $\bar{P} = 0.47$ and $\bar{H} = 0.15$. Other highly variable mollusks include *Crepidula onyx* ($P = 0.56$–0.70, $\bar{H} = 0.14$–0.17) (WOODRUFF *et al.*, 1986), *Nautilus pompilus* ($P = 0.50$–0.66, $\bar{H} = 0.10$–0.16) (WOODRUFF *et al.*, 1987), *Oncomelania hupensis* ($P = 0.52$–0.62, $H = 0.19$–

0.21) (WOODRUFF *et al.*, 1988), and *Partula mooreana* ($P = 0.74$, $\bar{H} = 0.17$) (JOHNSON *et al.*, 1986b). Similar high values characterize the other two species of *Cristilabrum* examined and *Turgenitubulus tanmurranus*. In contrast, *Ningbingia australis* ($P = 0.19$, $\bar{H} = 0.08$) is less variable than the typical mollusk and only one-third as variable as the other Ningbing endemics. Although from Figure 2 it would be tempting to suggest that *Ningbingia* may have been derived from a variable *Cristilabrum-Turgenitubulus* ancestor and lost its variation during its origination, morphological evidence strongly contradicts a *Turgenitubulus* to *Ningbingia* transition. The former genus has a "dead end" specialized genitalic complex, which is readily derivable from the structures seen in *Cristilabrum*, but very different from the *Ningbingia* pattern (Solem, unpublished). It is also important to remember that intraclade levels of polymorphism can be highly variable. Even within a genus two- to three-fold differences in polymorphism are not unusual: *e.g.*, within the genera mentioned earlier in this paragraph, *Crepidula adunca* ($P = 0.34$), *Nautilus macromphalus* ($P = 0.33$), *Oncomelania quadrasi* ($P = 0.20$), and *Partula exigua* ($P = 0.47$) (above-cited references). Further discussion of the reduced levels of variation in *Ningbingia* will have to await comparative data on other species in the radiation.

Despite the high levels of variation within populations only minor differences were detected between congeneric species. The three species of *Cristilabrum* share most of the same alleles and differ primarily in allelic frequencies (Table 2). No single locus distinguishes *C. primum* from *C. grossum* and only half the specimens of the latter taxon possess species-specific alleles (*Ldh*[d] and *Sord*[a]). Similarly, allelic frequency differences at four loci contribute most to the distinction between *C. primum* and *C. monodon*; alleles specific to the latter taxon were detected at 1–2 loci in only half the individual snails. Representatives of the other genera were more differentiated but still shared 53% (*Turgenitubulus*) or 26% (*Ningbingia*) of their alleles with *Cristilabrum*. NEI's (1978) unbiased genetic distance (D) is particularly useful for quantifying such allelic frequency-dependent differences. As the calculated values of D are low to moderate (0–0.59), and as the number of loci ex-

A

NEI'S GENETIC DISTANCE (*D*)

B

DISTANCE FROM ROOT

Figure 2

A. Phenetic tree based on variation at 21 loci. B. Wagner tree rooted with *Ningbingia australis* as the outgroup.

amined and the sample sizes are adequate (NEI, 1987), *D* should provide a reliable estimate of genetic differentiation in this group.

Although there is no simple linear relationship between Nei's *D* and level in a taxonomic hierarchy, some broad generalizations are possible. Within a clade *D* typically increases between populations, species, and genera. THORPE's (1983) survey of over 7000 published conspecific comparisons showed that 98% of the intraspecific *D* estimates were ≤0.10. In contrast, he found that among 900 interspecific congeneric comparisons *D* was typically about 0.40 (range: 0.03–>1.00). Similar results were obtained by WOODRUFF *et al.* (1988) in their survey of 20 molluscan genera: genetic distances between conspecific populations were typically *D* ≤ 0.10 and between congeneric species, *D* > 0.05 (typically 0.20–0.60).

In this light, the species of the Ningbing radiation are less well differentiated than might be expected. *Cristilabrum primum* and *C. grossum* (*D* = 0.04) are barely distinguishable at the 21 loci studied. *Cristilabrum monodon* is only moderately differentiated (*D* = 0.17) from its congeners. *Turgenitubulus* and *Ningbingia* differ from *Cristila-*

brum at levels more typical of other animal species than of genera (*D* = 0.27–0.50). There was, however, no reason to suppose that these previously unstudied camaenid taxa would show "typical" levels of genetic divergence; one of the main aims of the present report is to establish their clade-specific pattern.

Within *Cristilabrum primum* our comparison of the three samples revealed no significant differentiation. Genetic distance values ranged from zero to 0.016 and at this level of variation the standard errors of *D* exceed the *D*-values themselves (NEI *et al.,* 1985). This genetic homogeneity conforms with a pattern of conchological and genital stability; only adult shell size shows significant variation. The shells of *C. primum* average 16.25–17.05 mm in diameter where their shelter sites are exposed to morning (east side) or midday sun (north side), but average 19.58–20.53 mm, or 20% larger, when the shelter site faces south and is shaded almost the entire day. No geographic differences in genital structure were observed.

Comparing *Cristilabrum primum* with its neighbor to the south, *C. grossum,* we estimated *D̄* = 0.039 (0.026–0.051); values not significantly different from zero. One

Table 4

Summary of conchological and anatomical differences between three species of *Cristilabrum*.*

Character	C. monodon (n = 480)	C. primum (n = 1123)	C. grossum (n = 700)
Shell height (mm):	8.89 (7.4–10.5)	9.01 (7.2–12.75)	11.03 (9.05–13.4)
Shell diameter (mm):	17.37 (14.8–19.5)	17.29 (14.5–21.8)	20.72 (17.75–23.7)
No. of whorls:	5½ (5⅛–6)	4⅞+ (4⅜–5⅞+)	5⅜ (4⅞–6+)
Shell sculpture:	greatly reduced	very prominent above and below shell periphery	prominent above, reduced on base
Lip ridge on:	palatal wall	basocolumellar wall, recessed	basal wall
Palatal groove:	absent	weak	strong
Shell periphery:	rounded	sharply angled	weakly angled
Vagina/penis length	equal	equal	0.67
Free oviduct	very short	medium short	short
Penis apical plug	small	small	large
Penis stimulator	reduced	medium	large
Penis and sheath rel. length	1.3×	2×	4×
Penis sheath wall thickened	all	lower ⅓	lower ½

* Source: SOLEM, 1981, 1985, unpublished.

might conclude that the two taxa are really conspecific but this would be an error for several reasons. First, as mentioned above D values do not dictate taxonomic decisions. There are many other cases of very low interspecific genetic distances: for some sibling species of *Drosophila* $\bar{D}$ = 0.03 (PRAKASH, 1969; CARSON, 1982); for interspecific comparisons in many genera of birds $\bar{D}$ ≤ 0.05 (CORBIN, 1987). Turning to land snails, JOHNSON *et al.* (1986a) found interspecific genetic distances between four species of *Samoana* were D ≤ 0.03. In *Cerion*, three pairs of semispecies showed genetic distances of $\bar{D}$ = 0.05 (GOULD & WOODRUFF, 1978, 1986, 1987). Second, there is abundant evidence that *Cristilabrum primum* and *C. grossum* have acquired other attributes of good species. A number of shell and genital differences are listed in Table 4. It is highly significant that no structurally intermediate examples were seen among 2305 adult specimens examined for shell features. Differences in the absolute and relative sizes of terminal genital organs are equivalent to those seen in sympatric species pairs of *Cristilabrum* (see SOLEM, 1985) and thus indicate species-level differentiation. Although direct observational data are lacking, we hypothesize that the major differences in the genitalia play key roles in species isolation and recognition. Speciation thus appears to have involved significant changes in morphology but left the detectable genetic (allozymic) architecture unchanged. There is, of course, no reason to expect the evolution of morphological and behavioral traits to involve a concomitant differentiation at allozyme loci.

At the north end of its range, *Cristilabrum primum* is replaced by *C. monodon* (Figure 1C). Although similar in size and shape, they differ grossly in shell sculpture, whorl count, and penis-penis sheath structures (Table 4). They also are better differentiated allozymically. The genetic distance is $\bar{D}$ = 0.17 and there is no evidence of introgression between the samples collected 200 m apart on the same hill. *Cristilabrum monodon* occupies the northwest corner of the main mass, but also occurs alone on the large outcrop to the north. It is most similar in both genital anatomy and shell features to *C. bubulum,* which lives on limestone masses to the southwest of the *monodon-primum-grossum* habitat.

In this preliminary report we demonstrate the results of two different methods of clustering these taxa based on allozyme variation. First, using a phenetic approach we can cluster taxa solely on the basis of their average genetic distances (Figure 2A). This approach allows for the importance of changes in allele frequencies. The phenogram will not reflect phylogenetic relationships, however, unless it is assumed that the rates of evolutionary change have been constant among the lineages. If the expected rate of gene substitution is approximately constant among these related snails, then the measure of divergence employed, Nei's D, will be directly proportional to evolutionary time. In that case the UPGMA phenogram will give correct phylogenetic topology and branch lengths. It would, however, be premature to regard Figure 2A as a phylogenetic tree at this stage of our investigation.

An alternative approach to the problem of phylogenetic reconstruction is the Distance Wagner method (FARRIS, 1972) which we have used here with a metric, the modified Rogers' distance (WRIGHT, 1978). We studied mid-point rooted and out-group rooted trees and present one of the latter for discussion purposes (Figure 2B). It has been argued that if the taxa under consideration have a history of demographic bottlenecks then this algorithm should be preferred over the average distance method. Different branch lengths are presumed to reflect different rates of

change (FELSENSTEIN, 1984). The tree shown has been optimized (from among the more than 8000 possible trees relating 10 samples) and *Ningbingia australis* has been designated the outgroup for purposes of rooting the tree.

We share with SWOFFORD & BERLOCHER (1987) the view that allozyme frequencies are evolutionarily meaningful and that traditional cladistic methods that reduce the data by "presence/absence" coding are inferior. For this reason, we have not used a Hennigian approach to the genetic data. It is still important to heed FELSENSTEIN's (1982) admonition not to adopt a single method for inferring evolutionary trees until much more is known about the biological assumptions and statistical behavior of the various approaches.

We will postpone a detailed discussion of the phenetic and phylogenetic trees presented here until more species are added to the analysis. Suffice to say, we are able to distinguish the various taxa and produce biologically realistic hypotheses concerning their relationships. All trees cluster the taxa in a similar manner affirming the genetic affinities between *Cristilabrum primum* and *C. grossum* and the greater differentiation of their congener, *C. monodon*. *Turgenitubulus* is seen to cluster with *Cristilabrum* rather than *Ningbingia*. On the basis of fundamentally divergent stimulatory structures in the terminal genitalia, Solem (in preparation) considers that *Ningbingia* and *Cristilabrum* are not closely related to each other. It may be that they will cluster more closely with genera from elsewhere in Australia than with each other. In contrast, *Turgenitubulus* and *Cristilabrum* are very closely related. Unique derived genital features of the former can be derived from the latter, and some species show partly intermediate stages (Solem, in preparation).

A comparison of the original descriptions of the 28 species (in the genera *Ningbingia*, *Turgenitubulus*, *Cristilabrum*, and *Ordtrachia*) of endemic camaenids (SOLEM, 1981, 1985, 1988b, 1989b) suggests that the reconstruction of a phylogeny based on a cladistic analysis of anatomical variation may not be possible (Solem, in preparation). Numerous apparent cases of parallel evolution, convergent evolution, and reversal occur among the continuous morphological variables studied. In contrast, the allozymic data appear suitable for rigorous phylogenetic analysis. In subsequent papers we will develop evolutionary hypotheses based on the inclusion of additional endemic species and representatives of possible ancestral outgroups. Again, available anatomical data do not immediately identify a probable sister group to the Ningbing endemics elsewhere in northwestern Australia. Thus, allozymes will be used to establish alternative hypotheses for testing.

ACKNOWLEDGMENTS

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Comparative Zoogeography of Marine Mollusks from Northern Australia, New Guinea, and Indonesia

by

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Abstract. The shallow-water marine prosobranch mollusks occurring in northern Australia are compared with species living in adjacent areas of the Indo-West Pacific (Indonesia and New Guinea) based on an analysis of the presence or absence in each of the three areas of 977 species from 21 families of prosobranch gastropods. The fauna of northern Australia, while diverse, is generally considered less diverse than that which occurs in the biogeographic center of the Indo-West Pacific, the area bordered by the Philippines, Malaysia, and New Guinea. In the present study 754 species are known to occur in northern Australia, 625 in Indonesia, and 809 in New Guinea. If Indonesia and New Guinea are combined, 876 species are known to occur in the islands to the north of Australia, 16% more species than in Australian waters. With our uncertain knowledge of the taxonomy and distributions of individual species, this difference is not considered to indicate a reduced diversity in the marine shallow-water fauna of northern Australia.

Almost 92% of the mollusks studied occur in Indonesia and/or New Guinea; just over 8% are endemic to northern Australia. Slightly higher percentages of endemism (13%) occur in the two other best known, taxonomically diverse groups, echinoderms and fish. These data suggest that as the fauna becomes better known the reasons for recognizing a separate Tropical Australian Province in the Indo-West Pacific will be further reduced.

INTRODUCTION

The northern coastline of the continent of Australia, from North West Cape in Western Australia to the southern limit of the Great Barrier Reef in Queensland, has a tropical shallow-water marine fauna that is closely related to that which occurs in the central Indo-West Pacific (EKMAN, 1967). Further south on both the east and west coasts of Australia the fauna is a mixture of a decreasing proportion of tropical species, an increasing proportion of temperate species, and a group of species endemic to either the east or west coast.

Early studies (HEDLEY, 1926; WHITLEY, 1932) divided the marine fauna of the north coast of Australia into three provinces separated at Cape York in northern Queensland: the Dampierian Province of northwestern Australia, the inshore Banksian Province of Queensland, and the Solanderian Province, which encompassed the Great Barrier Reef off the Queensland coast. ENDEAN (1957), working on echinoderms, combined the inshore (Banksian) region of Queensland and the Dampierian Province as a Tropical

Australian Province across the entire north coast of the continent, but regarded the Great Barrier Reef as a distinct faunal region. As knowledge of the fauna of northwestern Australia improved several studies have concluded that there is no need to divide the coastline of northern Australia, and a single Tropical Australian Province which includes the Great Barrier Reef is recognized (WILSON & GILLETT, 1971; WELLS, 1980, 1986; WILSON & ALLEN, 1988).

The relationships of the tropical Australian coast to the traditional faunistic center of diversity in the Indo-West Pacific, the area bordered by a triangle connecting the Philippines, Malaysia, and Papua New Guinea (BRIGGS, 1975), are still uncertain. Northern Australia lies outside the triangle and while the fauna is diverse, it is not thought to equal the diversity of the central area (BRIGGS, 1975).

This paper has two goals: to examine faunal diversity in northern Australia to determine whether diversity is in fact less than in the traditional faunistic center of diversity and to examine the validity of separating northern Australia from the area to the north as a Tropical Australian Province.

MATERIALS AND METHODS

The same families of prosobranch gastropods examined in my previous papers (WELLS, 1980, 1986) are utilized for comparison. Gastropod species listed in previous papers from Western Australia (WELLS, 1980, 1986; WELLS & SLACK-SMITH, 1986), the works of HINTON (1972, 1978, 1980), WILSON & GILLETT (1971), ROBERTS *et al.* (1982), WELLS & BRYCE (1986), and SHORT & POTTER (1987), and the list of species I collected at Madang, Papua New Guinea, in 1987 were used to develop a composite list of species known to occur in the region. The collections of the Western Australian Museum (WAM) were searched to provide additional unpublished records. In addition to being strong in Western Australian material, the WAM collection has considerable Indonesian material collected during the Muriel King and Rumphius expeditions in the 1960s and 1970s. The literature was also examined for additional records; a complete list of reports used is included in the Literature Cited. Emphasis was placed on records from revisionary works such as REID (1986) and BRATCHER & CERNOHORSKY (1987) rather than more general works. Only records where a species was specifically listed from an area were used; distribution maps suggesting that the range of a species should include one of the three areas, but not specifying a locality, were disregarded. Additional records were provided by examining the collections of the Australian Museum, Sydney.

Species examined are all shallow-water animals that occur in depths of less than 50 m for at least part of their range. Species that occur only in deeper water are disregarded.

For the purposes of this paper the three geographic areas need to be defined. The paper is intended to compare the mollusks of three areas, but political boundaries do not always reflect zoogeographic regions. In addition some of the literature and specimen records list "Borneo" or "New Guinea" without specifying a more exact locality. Species included from northern Australia are those that have been recorded at some point from the area between North West Cape in Western Australia and the southern extremity of the Great Barrier Reef on the east coast. The continental shelf atolls of Rowley Shoals, Scott Reef, Seringapatam Reef, and Ashmore Reef off northern Western Australia and records from the Australian islands of Torres Strait are included. A small component (<5%) of the fauna of northern Australia consists of temperate and east and west coast endemic species that reach into the southern portions of the tropical areas; these have been ignored in the present paper. The Torres Strait islands belonging to Papua New Guinea and also New Britain Island are included in the New Guinea list. The New Guinea list covers all of the island of New Guinea, including the western half, which is the Indonesian province of Irian Jaya. The islands to the west of New Guinea and the remainder of the Indonesian Archipelago are included in Indonesia. Most of the island of Borneo is Indonesian, though the northern por-

tion is part of Malaysia. For the purposes of this paper all records from Borneo are included in the Indonesia category.

An index of similarity (KREBS, 1978) was used to compare species overlap between the various areas. The formula is $I = \dfrac{2c}{a + b}$, where a is the number of species in area a, b the number in area b, and c the number of species in common. The index ranges from 0 if there are no species in common to 1 if the overlap is total.

RESULTS

A total of 977 prosobranch gastropod species in the 21 families were recorded in at least one of the three regions. The most diverse families are the Conidae with 127 species, Mitridae (109), Terebridae (94), Costellariidae (95), Cypraeidae (87), and Nassariidae (84). The high diversity in these families is probably not an artifact of collecting data, but is partly due to numerous records that have resulted from recent revisions by CERNOHORSKY (1976: Mitridae), CERNOHORSKY (1984: Nassariidae), and BRATCHER & CERNOHORSKY (1987: Terebridae) and shell books by WALLS (1980: Conidae); PECHAR *et al.* (1980: Mitridae and Costellariidae), and BURGESS (1985: Cypraeidae). Together the five families have 596 species, 61% of the total examined. Some of the families that are not popular with shell collectors and have not been recently revised are probably underrepresented. For example only 25 species of Trochidae are included. These are primarily species with large shells such as those of the genera *Trochus* and *Tectus*, but species with smaller shells such as *Clanculus* are not fully covered. For these reasons the diversity of the various families should be considered to be only relative. These problems are probably characteristic of all three areas, and although northern Australia is better collected than the others, the general trends should be valid. Most of the species occurred in more than one of the three areas: 474, or 48.5% in all three; 251, or 25.7% in two; 252, or 25.8% in only one area (Table 2).

There are 754 species in northern Australia compared to 625 for Indonesia and 809 for New Guinea (Table 1). Thus New Guinea has 7% more species than northern Australia, but 17% fewer species are known to occur in Indonesia. If northern Australia (754 species) is compared with New Guinea and Indonesia combined (876), New Guinea-Indonesia has only 122, or less than 16% more species than the northern Australian coastline.

Ninety-six of the species examined were recorded only from Australian waters, raising the possibility that they are endemic to tropical Australia. Thirty-three of these are known to occur in Indo-West Pacific areas elsewhere than Indonesia-New Guinea. These species may also be found in Indonesia-New Guinea, but no records could be located. Most of the remaining 63 species are probably Australian endemics; this indicates that a maximum of

Table 1

Number of shallow-water species of 21 families of gastropod mollusks recorded from three geographical areas. Abbreviations: AUS, northern Australia; NG, New Guinea; IND, Indonesia; TOT, total; ISL, islands (combination of New Guinea plus Indonesia); END, species possibly endemic to Australia.

Family	Number of species									
	AUS	NG	IND	TOT	AUS-NG	AUS-IND	NG-IND	ISL	AUS-ISL	END
Haliotidae	6	5	4	6	5	4	4	5	5	1
Trochidae	24	20	16	25	19	15	15	21	20	2
Turbinidae	17	13	12	20	12	9	9	16	13	2
Neritidae	10	8	10	10	8	10	8	10	10	0
Littorinidae	18	16	21	28	13	12	14	23	13	5
Strombidae	35	37	36	39	34	32	35	38	34	0
Naticidae	24	20	17	25	19	17	16	21	20	2
Cypraeidae	73	72	66	87	68	59	61	77	69	1
Cassidae	9	10	11	11	9	9	10	11	9	0
Tonnidae	9	10	6	11	8	6	5	11	9	0
Muricidae	44	38	21	53	30	18	18	41	32	8
Thaididae	43	35	36	44	35	36	29	42	42	1
Columbellidae	14	11	11	15	10	11	9	13	12	1
Nassariidae	50	57	47	84	40	38	46	78	44	4
Fasciolariidae	26	21	16	27	21	15	15	22	22	2
Olividae	23	30	27	35	21	19	24	33	21	1
Mitridae	83	102	69	109	77	56	56	105	79	2
Costellariidae	59	93	43	95	57	35	43	93	57	1
Volutidae	28	8	9	32	6	7	3	14	10	21
Conidae	93	108	87	127	81	70	74	117	85	5
Terebridae	66	65	60	94	52	42	40	85	57	4
Totals	754	809	625	977	625	520	534	876	663	63

8.3% are endemics. Of the 63 species, 21, or one-third are volutes (Table 1).

DISCUSSION

The data presented above once again demonstrate, at least for mollusks, the close affinity between the shallow-water marine fauna of the coastline of northern Australia and the adjacent areas (Indonesia and New Guinea) of the Indo-West Pacific. The great majority (74%) of the species examined are known to occur in more than one of the three areas analyzed. All of the authors of zoogeographical papers examined (CLARK, 1946; ENDEAN, 1957; KNOX, 1963, 1980; BRIGGS, 1975; MARSH, 1976; WILSON & STEVENSON, 1977; WELLS, 1980, 1986; MARSH & MARSHALL, 1983) agree that the marine shallow-water fauna of northern Australia is part of the Indo-West Pacific.

The close relationship between the fauna of northern Australia and the islands to the north is not surprising. A full range of marine shallow-water habitats is in the two areas, including mangroves, coral reefs, rocky and sandy intertidal and subtidal areas, and estuaries. The ocean is shallow between Australia and New Guinea and Indonesia, with land bridges existing during several periods of lowered sea levels during the Pleistocene. The most recent time during which there was a land bridge across Torres

Strait was between 8000 and 6000 years BP (MARSH & MARSHALL, 1983). Even today, with Australia separated by oceanic waters from Indonesia and New Guinea, a series of islands allows ready distribution between areas by species with planktonic larval stages.

Two questions remain to be addressed: is the fauna of northern Australia less diverse than that of the faunistic center of the central Indo-West Pacific (the Philippines-Malaysia-New Guinea triangle of BRIGGS [1975]) and is the fauna of northern Australia sufficiently distinct to be regarded as a separate zoogeographical province?

For the 21 families of prosobranch gastropods examined the total number of species known to occur in Indonesia-New Guinea is 16% greater than those known to live in northern Australia. Two problems arise in evaluating this figure. First, the data cannot be statistically tested. However, the figure of 16% itself is not substantial. I know of no other quantitative comparison, either in mollusks or other groups, of the fauna of northern Australia with the adjacent areas of the Indo-West Pacific to which the figure can be compared. The second problem is that the data are obviously incomplete—further collecting in all of the three areas will undoubtedly reveal new records. Most of the families have not recently been revised, and future revisions will change our concepts of at least some of the species involved, perhaps resulting in the synonymizing of some

Table 2

Number of geographic regions in which shallow-water species of 21 families of gastropod mollusks have been recorded.

Family	Number of regions			
	Three	Two	One	Total
Haliotidae	4	1	1	6
Trochidae	14	7	4	25
Turbinidae	8	6	6	20
Neritidae	8	2	0	10
Littorinidae	12	3	13	28
Strombidae	30	7	3	39
Naticidae	15	6	4	25
Cypraeidae	58	14	15	87
Cassidae	9	1	1	11
Tonnidae	5	4	2	11
Muricidae	16	18	19	53
Thaididae	29	12	3	44
Columbellidae	9	3	3	15
Nassariidae	33	23	28	84
Fasciolariidae	14	8	5	27
Olividae	19	7	9	35
Mitridae	54	31	24	109
Costellariidae	34	32	29	95
Volutidae	2	9	21	32
Conidae	64	31	32	127
Terebridae	37	26	31	94
Totals	474	251	252	977

taxa now regarded as sibling species but alternatively possibly resulting in the separation of what is now considered to be one species into two or more. In view of these difficulties the figure of 16% for the gastropod families examined is not sufficiently large to justify the statement that the fauna of northern Australia is less diverse than the central area of the Indo-West Pacific.

The concept of a Tropical Australian Province is generally recognized (ENDEAN, 1957; MARSH, 1976; WELLS, 1986), but there are few data on the level of endemicity of marine groups in northern Australia. The level of endemicity required for a region to be considered distinct is arbitrary, but BRIGGS (1975) suggests a level of 10%. The data presented above show that 754 species of shallow-water gastropods in 21 families occur in northern Australia. At most 63, or 8%, are endemic to the north coast and one-third (21 species) belong to the single family Volutidae. Three-fourths (75%) of volute species examined are endemic to northern Australia. The next highest proportion of Australian endemics is in the littorinids with 27%. Volutes deposit their eggs in benthic egg masses from which the young hatch as crawling juveniles (WILSON & GILLETT, 1971). The high proportion of volute species endemic to Australia is not surprising in view of the lack of a planktonic distributional phase in this group. Thus the shallow-water gastropods are near to, but below, the 10%

level of endemicity required by BRIGGS (1975) to recognize the Tropical Australian Province.

MARSH & MARSHALL (1983) presented data on 376 shallow-water echinoderm species, 49 (13%) of which were regarded as endemic to northwestern Australia. The 1983 data contrast with the finding by MARSH (1976) only seven years earlier that 22 of 114 (19%) asteroid species examined were endemic to the state. MARSH & MARSHALL (1983) cautioned that with improved knowledge of the taxonomy of the species involved the level of endemicity might be further reduced. In such a short time the level of perceived endemicity has been reduced as knowledge of the fauna improved. This lower actual endemicity was confirmed by the report of MARSH (1986) of an additional 14 species of shallow-water echinoderms from northwestern Australia; all are Indo-West Pacific species. WILSON & ALLEN (1988) recently analyzed distributions of shallow-water fish in northern Australia. Of the approximately 2000 known species 13% are endemic to northern Australia. The data for the three major faunal groups show that the case for separation of the Tropical Australian Province from the remainder of the Indo-West Pacific is marginal. HEDLEY's (1926) concept of the north coast as a separate geographical province has been undermined in recent years by an increased understanding of the close relationship between the fauna of the north coast and the remainder of the Indo-West Pacific.

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New Records for Western Pacific *Morum* (Gastropoda: Harpidae) with Biogeographic Implications

by

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Abstract. Major extensions of the known range are reported for six species of the prosobranch genus *Morum*, namely: *M. teramachii*, *M. uchiyamai* and *M. joelgreenei* in the Mariana Islands, *M. uchiyamai* and *M. bruuni* in the region of New Caledonia, *M. cancellatum* in the Fiji Islands, and *M. kurzi* in the Solomon Islands. The distributional patterns of the 15 recognized species of *Morum* living in the Indo-West Pacific biogeographic region are evaluated in terms of the occurrences of these taxa on the regional lithospheric plates. The fossil and modern distributional patterns of *Morum* (*sensu lato*) suggest that these gastropods are remnants of a Tethyan faunal element which is limited in distribution owing largely to the apparent lack of teleplanic larvae.

INTRODUCTION

This paper records major extensions of the known range for six Indo-Pacific species of the genus *Morum*. Specimens of *Morum teramachii* Kuroda & Habe, 1961, *M. uchiyamai* Kuroda & Habe, 1961, and *M. joelgreenei* Emerson, 1981, were obtained in the Mariana Islands by deep-water shrimp trapping operations of the NOAA vessel *Townsend Cromwell* during 1982 to 1984. This survey was conducted by the National Marine Fisheries Service, Southwest Fisheries Center Honolulu Laboratory as part of their Resource Assessment Investigation of the Mariana Archipelago Program (EMERSON & MOFFITT, 1988). Specimens of *Morum bruuni* (Powell, 1958) and *M. uchiyamai* Kuroda & Habe were dredged in 1986 off New Caledonia in deep water by the N.O. *Vauban* and N.O. *Coriolis,* vessels operated by the ORSTOM Center in Nouméa, New Caledonia (BOUCHET, 1986; RICHER DE FORGES, 1988). A single specimen of *M. kurzi* Petuch, 1979, was collected in 1985 by SCUBA diving from off Guadacanal in the Solomon Islands. A specimen of *M. cancellatum* B. G. Sowerby I, 1824, inhabited by a hermit crab was taken in a baited trap off Suva Reef, Fiji Islands, in 1979.

These new records significantly extend the known ranges of these taxa eastward along the Eurasian, Philippine, and Indian-Australian Lithospheric Plates to the western margin of the Pacific Plate.

ABBREVIATIONS

The following abbreviations for institutions and organizations are used in the text.

AMNH—American Museum of Natural History, New York

BM(NH)—British Museum (Natural History), London

MNHN-Paris—Muséum National d'Histoire Naturelle, Paris

NMFSHL—National Marine Fisheries Service Southwest Fisheries Center, Honolulu Laboratory
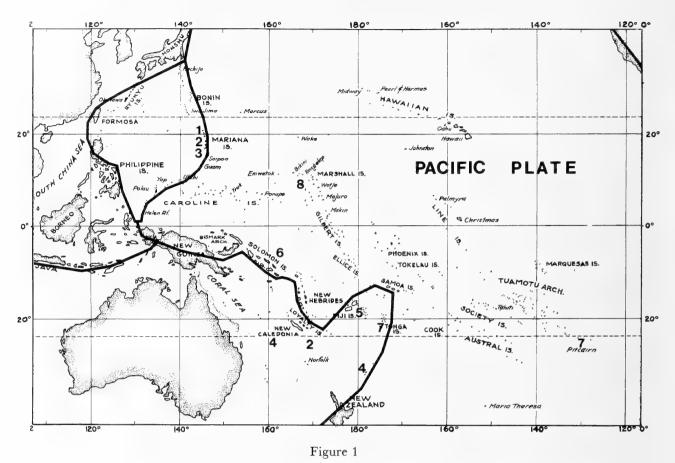
NMNH—National Museum of Natural History, U.S. National Museum collection (USNM), Smithsonian Institution, Washington, D.C.

ORSTOM—Institut Français de Reserches pour le Développement en Coopération, Paris and Nouméa

TC—National Oceanic and Atmospheric Administration vessel *Townsend Cromwell*

UGMLM—University of Guam, Marine Laboratory, Mangilao, Guam

USBF—United States Bureau of Fisheries

Figure 1

Distribution of *Morum* on the Pacific Plate (species numbers 6–8) and on or near the border of the Pacific Plate (species numbers 1–5, 7). 1 = *M. teramachii*, 2 = *M. uchiyamai*, 3 = *M. joelgreenei*, 4 = *M. bruuni*, 5 = *M. cancellatum*, 6 = *M. kurzi*, 7 = *M. ponderosum*, and 8 = *M. macdonaldi*. (Base map, without the plate boundaries, courtesy of R. T. Abbott.)

SYSTEMATIC TREATMENT

Family HARPIDAE Bronn, 1849
Subfamily MORUMINAE Hughes & Emerson, 1987
Genus *Morum* Roeding, 1798
Subgenus *Oniscidia* Moerch, 1852

Morum (O.) cancellatum G. B. Sowerby I, 1824

(Figures 6, 7)

New record: FIJI ISLANDS: off Suva Reef (18.05°S, 178.25°E), Viti Levu in 220 m (120 fms), 21 March 1979, in baited *Nautilus* trap, 1 crabbed specimen, Roper and Sweeney collectors (USNM 773946).

Remarks: This record is based on a single, well-preserved, hermit-crabbed specimen, with fully developed apertural dentition and parietal shield (Figures 6, 7). The present specimen (44.1 mm × 27.5 mm) is slightly smaller than the lectotype, which measures 47.2 mm in height and 28.6 mm in width [BM(NH) 197744, EMERSON, 1985:54, figs. 17, 18], but is otherwise typical of this species.
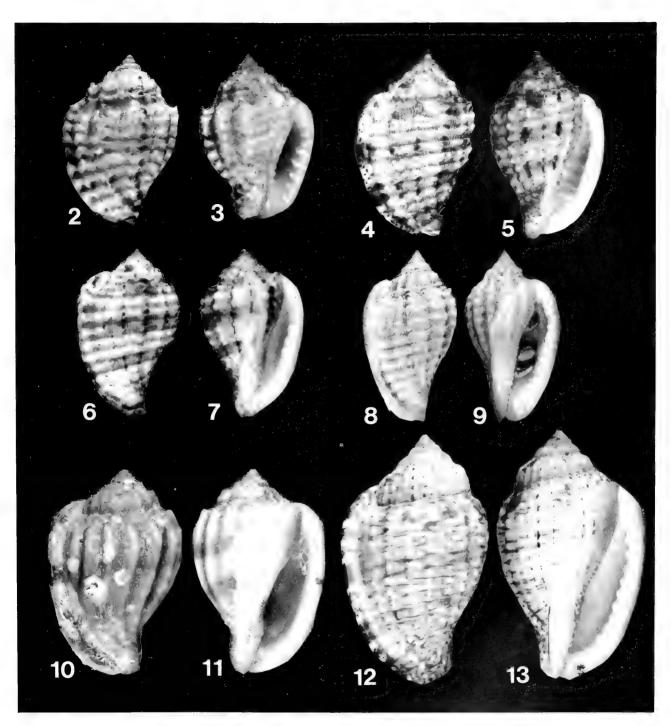
Range: Previously known from southern Japan, Taiwan, the south China coast (off Pratas Island, in 161 m [88 fms], USBF Sta. 5111 (USNM 232801, USNM 237710), and the central Philippine Islands (Sandugan Pt., Signjos, Mindoro Island, AMNH 207315). Here recorded from the Fiji Islands in 220 m (dead specimen).

Morum (O.) joelgreenei Emerson, 1981

(Figures 4, 5)

Synonym: *M. (O.) celinamarumai* Kosuge, 1981 (see EMERSON, 1985: 52, pl. 1, figs. 9, 10). **Type locality:** "Bohol, Philippines."

New record: MARIANA ARCHIPELAGO: off Pagan Island (18°04.8′N, 145°45.2′E), in 201–284 m (110–150 fms), TC 84-02, Sta. 3, 20 February 1984 (AMNH 232122), from shrimp trap, 1 crabbed specimen.

Remarks: The present specimen (Figures 4, 5) is well preserved, but small (measuring 32 mm in length and 20.3

Explanation of Figures 2 to 13

Figures 2–13. Specimens representing the six taxa of *Morum* (*Oniscidia*) for which significant range extensions are recorded in this paper. Figures 2, 3: *M. kurzi* (AMNH 213436); ×2. Figures 4, 5: *M. joelgreenei* (AMNH 232122); ×1. Figures 6, 7: *M. cancellatum* (USNM 773946); ×1. Figures 8, 9: *M. uchiyamai* (AMNH 232123); ×1. Figures 10, 11: *M. bruuni* (Station DW71, MNHN-Paris); ×1.5. Figures 12, 13: *M. teramachii* (AMNH 232124); ×1.

mm in width) with an incompletely developed outer lip and an immature parietal shield.

Range: Previously known from moderately deep water (100 to 150 m) off the southern Philippine Islands. Here recorded from the Mariana Islands in deeper water (dead specimen).

Morum (O.) kurzi Petuch, 1979

(Figures 2, 3)

New record: SOLOMON ISLANDS: 1 km west of Honiara, Guadacanal Island, in 25–30 m (14–17 fms), spring of 1985, 1 specimen, by SCUBA diving, Johnson Kengalu collector (AMNH 213436).

Remarks: On a collecting trip to the Solomon Islands, Don Pisor obtained a single, live-collected specimen from a local diver (Figures 2, 3). It is typical of the Philippine specimens (type locality off Panglao, Bohol Island) and is essentially the same size as the holotype (EMERSON, 1985: 53, pl. 1, figs. 5, 6). The present specimen was generously donated to the AMNH by Mr. Pisor.

Range: Previously known only from the southern Philippines in depths of 110 (AMNH 213707) to 250 m (PETUCH, 1979). Here recorded from the Solomon Islands in lesser depths (25–30 m).

Morum (O.) teramachii
Kuroda & Habe *in* Habe, 1961

(Figures 12, 13)

New records: MARIANA ARCHIPELAGO: off Pagan Island (15°01′N, 145°14′E), in 366 m (220 fms), TC 82-04, Sta. 31, 3 August 1982 (AMNH 232126), from shrimp trap, 1 crabbed specimen; off Anatahan Island (16°21.6′N, 145°43.9′E), in 353 m (193 fms), TC 82-02, Sta. 47, 28 April 1982 (AMNH 232127), from shrimp trap, 2 live-taken specimens; off Farallon de Medinilla (16°08′N, 146°07′E), in 366 m (200 fms), TC 82-03, Sta. 104, 20 June 1982 (AMNH 232128), from shrimp trap, 1 crabbed specimen; off Arakane Reef (15°37.4′N, 142°46.2′E), in 311–476 m (170–260 fms), TC 83-05, Sta. 142, 15 December 1983 (UGMLM, No. 1; AMNH 232129, Nos. 3, 4), from shrimp traps, 4 crabbed specimens, No. 2 (AMNH 232124) here illustrated (Figures 12, 13); off Arakane Reef (15°37.6′N, 142°46.1′E) in 311–476 m (170–260 fms), TC 83-05, Sta. 151, 17 December 1983, USNM 869025, from shrimp trap, 1 crabbed specimen; off Esmeralda Island (15°01′N, 145°14′E), in 357–448 m (195–245 fms), TC 82-03, Sta. 39, 11 June 1982 (AMNH 232130), from shrimp trap, 1 crabbed specimen.

Remarks: The shells of the 10 specimens reported here range in measurements from 63.1 mm in length and 34.1 mm in width with 6½ post-nuclear whorls, to 40.9 mm in length and 26.4 mm in width with 5½ post-nuclear whorls.

The figured type specimen of this taxon was stated to measure 55.5 × 32.3 mm and was dredged off Cape Ashiuri, Kochi Pref., Shikoku, Japan, in ca. 200 m (INABA & OYAMA, 1977:121).

Range: Previously known from southern Japan and the southern Philippine Islands (GLASS & FOSTER, 1986:68) in moderately deep water (100–200 m). Here recorded from the Mariana Islands, in depths of 170–448 m (live-taken specimens from 353 m).

Morum (O.) uchiyamai Kuroda & Habe
in Habe, 1961

(Figures 8, 9)

New records: MARIANA ARCHIPELAGO: off Saipan Island (15°15.83′N, 145°41.10′E), in 366–384 m (200–210 fms), TC 81-01, Sta. 179, 13 April 1981 (AMNH 232123), from shrimp trap, 1 crabbed specimen here illustrated (Figures 8, 9); off Esmeralda Bank (15°01.8′N, 145°13.7′E), in 384–430 m (210–235 fms), TC 84-01, Sta. 16, 8 January 1984 (UGMLM), from pipe dredge, 1 dead and discolored specimen. SOUTH OF NEW CALEDONIA: (22°53′S, 167°11′E) in 375–402 m (206–221 fms), N.O. *Vauban* SMIB2 cruise, Sta. DW15, 18 September 1986, MNHN-Paris, 1 crabbed specimen, Menou and Tirard collectors; (21°01′S, 167°27′E) dredged in 250 m (138 fms), R.V. *Alis* MUSORSTOM 6, Sta. DW453, 20 February 1989, MNHN-Paris, 1 live-collected specimen, Bouchet and Richer de Forges collectors.

Remarks: All three of the dead-taken specimens are smaller than the type specimen (51.5 mm × 27.5 mm), which was dredged off Kochi Pref., Shikoku, Japan, in 200–300 m (INABA & OYAMA, 1977:128). The live-taken New Caledonia specimen (52.2 × 28.4 mm) specimen is approximately the size of the holotype. The largest Marianan specimen (45.1 mm × 24.9 mm) is illustrated.

Range: Previously known from the region of the East China Sea (southern Japan and Taiwan) in moderately deep water (183–300 m). Here recorded in the Mariana Islands and in the region south of New Caledonia, in depths of 200–250 m (living specimens from 250 m).

Morum (O.) bruuni (Powell, 1958)

(Figures 10, 11)

Synonym: *Pulchroniscia delecta* Garrard, 1961 (see BEU, 1976: 225–229, figs. 1, 2, 4, 5, 11–15).

New records: CORAL SEA: off New Caledonia (22°48′S, 159°24′E), dredged in 360–390 m (198–215 fms), N.O. *Coriolis*, MUSORSTOM 5 Cruise, Sta. 299, 11 October 1986, MNHN-Paris, dead specimen encrusted with barnacles, etc., Bouchet, Metivier and Richer de Forges collectors. SOUTH OF NEW CALEDONIA: (24°42′S, 168°10′E), dredged in 230 m (127 fms), N.O. *Coriolis* CHALCAL 2

Cruise Sta. DW71, 27 October 1986, MNHN-Paris, 1 dead specimen, Bouchet, Metivier and Richer de Forges collectors (Figures 10, 11). (24°45'S, 168°09'E), dredged in 230 m (127 fms), N.O. *Coriolis* CHALCAL Cruise 2, Sta. CP20, 27 October 1986, MNHN-Paris, 1 dead specimen, Bouchet, Metivier and Richer de Forges collectors.

Remarks: The aperture of each of the three specimens shows some wear and the shells may have been occupied by hermit crabs after the death of the snails.

Range: Previously known only from moderately deep water (137–154 m) off southeastern Australia (New South Wales) and the Kermadec Islands (north of New Zealand). Here recorded from the Coral Sea and off New Caledonia, in depths of 230 and 390 m (based on dead specimens).

BIOGEOGRAPHICAL CONSIDERATIONS

The genus *Morum* (*sensu lato*) was more widely distributed during the Tertiary with species known from the Paleogene of southern Europe, India, and Java, and from the Neogene of southern Europe, Japan, New Zealand, and the middle Americas. The surviving members of the subgenera *Oniscidia* and *Herculea* are most numerously represented in the western Pacific Ocean (see range data in Table 1). Here most of the species live at moderate shelf-depths to upper slope-depths, ranging from southern Japan, the Ryukyu Archipelago, Taiwan, and the southern Philippines. In the south Pacific, a few species are known from off southeastern Australia, New Zealand, New Guinea, New Caledonia, in the Solomon, Fiji and Tonga Islands, and at Pitcairn Island, occurring in depths of 25 to 350 m. Elsewhere in the Pacific Basin, a single species of *Oniscidia* is known in Micronesia (Marshall Islands) and two occur in the tropical eastern Pacific at Cocos Island and in the Galápagos Islands. One species of this subgenus is known from the western Indian Ocean and another in the Andaman Sea. The only other members of *Oniscidia* are known from the tropical western Atlantic, where three or four species are now recognized. *Morum* (*sensu stricto*) is limited to the New World tropics, with the oldest records dating from the Plio-Pleistocene. Three species of the nominate subgenus survive, two in the Caribbean region and one in the eastern Pacific, in shallow depths.
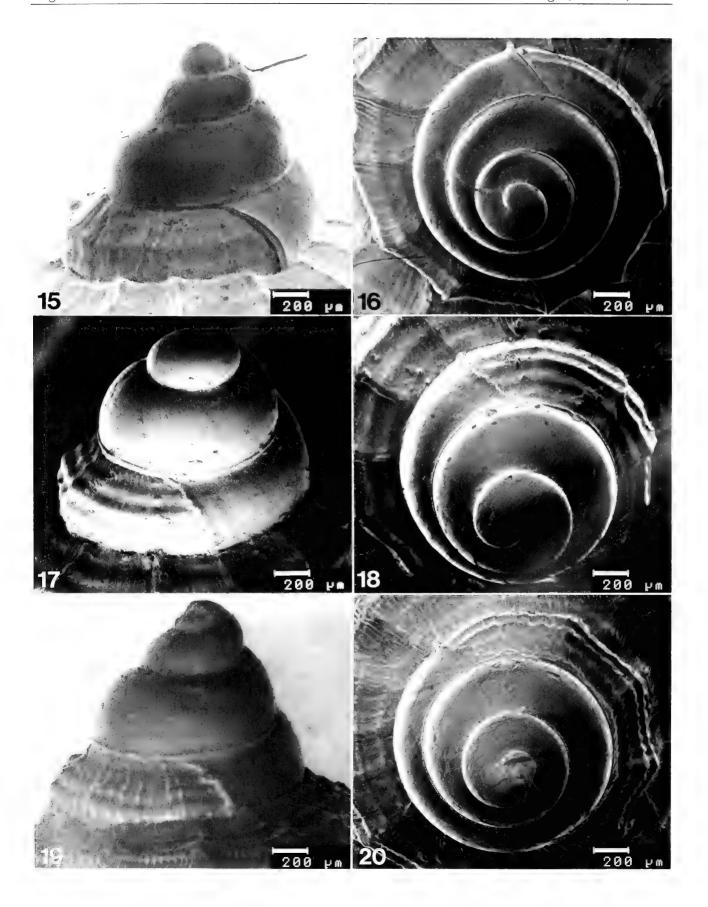
The fossil and modern distribution of *Morum* (*sensu lato*), therefore, suggests that these gastropods are remnants of a Tethyan faunal element with somewhat limited biological dispersal potential. Although data on larval development in *Morum* are meager, these gastropods apparently do not have teleplanic larvae. *Morum* (*Morum*) *oniscus* (Linnaeus, 1767) has a non-pelagic developmental mode. In this species, the large eggs are few in number and the juveniles emerge from the capsule at the crawling stage, with a protoconch of about 2.2 mm in height and with about 1½ to 2 nuclear whorls (WORK, 1969:657, fig. 2; HUGHES & EMERSON, 1987:357, fig. 7). Living representatives of the subgenera *Oniscidia* and *Herculea,* however,

Figure 14

A living specimen of *Morum* (*O.*) *macdonaldi,* the only known "Pacific Plate" species of *Morum,* from Kwajalein Atoll, Marshall Islands; about 5 times natural size. (Drawing by Nancy Tunnell, 1988; courtesy of D. J. MacDonald.)

have larger multiwhorled protoconchs (ABBOTT, 1968:20, pl. 5). Some have 3 to 3½ nuclear whorls and a flared lip which demarcates the protoconch from the teleoconch (Figures 15–20). Dr. M. G. Harasewych examined the protoconch of a specimen of *M. kurzi* (AMNH 213707; Figures 15, 16) and inferred this species to be at least lecithotrophic with a limited pelagic phase and possibly planktotrophic, on the basis of the morphology of the protoconch. He concluded: "Analysis by SHUTO's (1974) criteria [developmental mode inferred by ratio of the maximum diameter (D) to the number of protoconch whorls (VOL)] is inconclusive (VOL = 3.0; D = 1.41 mm; D/VOL = 0.47)" (Harasewych, *in litt.,* 15 May 1989). Dr. Rudolf S. Scheltema commented on the protoconchs of the three species figured herein as follows: "*Morum kurzi* (Figs. 15–16) has a planktotrophic veliger larvae as is inferred from the diameter of the apical protoconch whorl (ca. 220 μ by my measurement using the scale) and from the varix on the outer lip (which allows a rough estimate of size at settlement). The mode of development of *Morum bruuni* (Figs. 17–18) is less explicable; the rather large initial whorl (400 μ) probably indicates a direct development, presumably within the egg capsule. *Morum ponderosum* (Figs. 19–20) also must have a planktotrophic veliger. Judging by the size at settlement (estimated from the SEM micrographs) both *M. kurzi* and *M. ponderosum* probably have a planktotrophic development of at least one month (probably even 2). While 2 months is somewhat less than that of most teleplanic larvae, it nevertheless will allow considerable opportunity for passive dispersal by advection of ocean currents and may explain why *M. ponderosum* occurs on Pitcairn Island (a geologically young island of

15

200 µm

16

200 µm

17

200 µm

18

200 µm

19

200 µm

20

200 µm

less than 1 my) for which otherwise there is no ready explanation" (Scheltema, *in litt.,* 19 July 1989). The restricted distributional patterns indicated for other species, however, may reflect the presence of temporally limited pelagic larval stages.

The occurrences on the lithospheric plates for the 16 nominal species of *Morum* living in the Indo-West Pacific biogeographical region are tabulated (see Table 1). One of these taxa, *M. watsoni* Dance & Emerson, 1967, a new name for *M. cithara* (Watson, 1881), not *M. cythara* (Brocchi, 1814), was based on an immature specimen for which the taxonomic status is not certain. Of the remaining 15 taxa, 10 occur on the Eurasian Plate, whereas 7 or possibly 8 of these extend onto the adjacent Philippine Plate, and 3 of these also occur on the Indian-Australian Plate. Two taxa are limited, respectively, to the Indian-Australian Plate and the African Plate, and two are restricted to the Eurasian Plate. The remaining taxa are of special biogeographical interest and are discussed in more detail below.

Only 3 of the 15 recognized species (20%) are known from the Pacific Plate (Figure 1). One of these, *Morum macdonaldi,* occurs only at Kwajalein Atoll, Marshall Islands, where living specimens have been observed by SCUBA divers in 15–30 m off the exposed side of fringing reefs (Figure 14). This is the only known "low island" species. It may have been overlooked elsewhere owing to the small size of the shells (10–18 mm) and to a nocturnal habit. The same circumstances may be true for *M. kurzi,* which is well known from the southern Philippines (Philippine Plate) in tangle-net collections and is reported here from 25–30 m at Guadalcanal Island, Solomon Islands (Pacific Plate). Populations of one species, *M. ponderosum,* are apparently isolated on the Pacific Plate at Pitcairn Island, where they occur in depths to 110 m (USNM 789326). This taxon is also known from the Tonga Islands (CORNFIELD, 1986:9), New Caledonia (BOUCHET, 1981; BM[NH] 1964504), off Queensland, Australia (BEU, 1976:224) on the Indian-Australian Plate, and from the Ryukyu Archipelago (EMERSON, 1977:85) on the Philippine Plate.

As indicated above, only 1 of the 15 western Pacific species (*Morum macdonaldi*) is restricted to the Pacific Plate (Figure 1) and, thus, can be termed a "Pacific Plate species" (*cf.* SPRINGER, 1982; KAY, 1980, 1984; NEWMAN, 1986; BRIGGS, 1987). In three cases—*M. teramachii, M. uchiyamai,* and *M. joelgreenei*—species occur on the eastern border of the Philippine Plate in the Mariana Islands, but the deep Mariana Trench apparently prevents the non-planktotrophic larvae of these gastropods from reaching the Pacific Plate. This is in contrast to the Mariana shoal-water faunal elements with apparent teleplanic larval development, which are believed to be a major source via a dispersal pattern for planktonically derived northwestern constituents in the Hawaiian fauna. As VERMEIJ *et al.* (1983) have noted, an offshoot of the Kuroshio Current forms a countercurrent and flows through the northern Mariana Islands, continues eastward to near Johnson Island, and eventually reaches the northwestern Hawaiian Islands (*cf.* ZINSMEISTER & EMERSON, 1979). Thus, the Mariana Trench does not seem to be a barrier for passive dispersal of hemipelagic organisms that apparently have established Pacific Plate populations via the Marianas. The expansive deep-water barrier between the Mariana Islands and the Hawaiian Archipelago does, however, serve to select against the dispersal westward of certain molluscan groups, especially archaeogastropods and intertidal species (VERMEIJ *et al.,* 1983).

The Marianas apparently originated in the mid-Paleogene to the south and perhaps west of their present position, *i.e.,* closer to the Indonesian-Philippine arc systems (KARIG, 1975). Accordingly, the distance required for dispersal of continental species to the proto-Marianas would have been reduced. Perhaps other islands (now subducted) on the Pacific Plate could have served as stepping stones for colonization by larval dispersal of the more westerly situated islands on the Pacific Plate during the Neogene (SPRINGER, 1982).

The other two species of *Morum* known from the Pacific Plate are *M. kurzi* and *M. ponderosum* (Figure 1). The former occurs in the Solomon Islands adjoining the border of the Indian-Australian Plate. It is not known from the neighboring Bismarck Archipelago and the New Hebrides Islands (Vanuatu), which also border the Indian-Australian Plate. Collections from these areas, however, are not extensive. The vast Solomon Trench may act as a barrier for dispersal into the Melanesian region for species that undergo intracapsular metamorphosis or have a brief larval stage. The presence of *M. ponderosum* in the Tonga Islands on the far western border of the Indian-Australian Plate may reflect the survival of populations that were established on the Lau-Tonga Ridge, which may have been continuous with Kermadec Island Ridge (SPRINGER, 1982). This ridge fronts a deep trench on the east face and extends southwestward to near New Zealand. This may have also served as the dispersal pathway to account for the presence of *M. bruuni* in the Kermadec Islands. *Morum cancellatum*

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Explanations of Figures 15 to 20

Figures 15–20. Scanning electron micrographs showing lateral (left) and apical (right) views of three species of *Morum;* ×50. Figures 15, 16: *M. (O.) kurzi,* off Davao, Mindanao Island, Philippines (AMNH 213707). Figures 17, 18: *M. (O.) bruuni,* south of New Caledonia, 24°45′S, 168°09′E (MNHN-Paris). Figures 19, 20: *M. (H.) ponderosum,* off Seragaki Beach, Okinawa (AMNH 203693).

Table 1

Lithospheric Plate distribution of *Morum* in the Indo-West Pacific Tropics.

	1 African	10 Eurasian	9 Philippine	6 Indian-Australian	3 Pacific
n = taxa per plate					
Genus *Morum* Roeding, 1798					
Subgenus *Oniscidia* Moerch, 1852					
1. *M. amabile* Shikama, 1973					
Taiwan and ?Philippine Islands		X	X		
2. *M. bruuni* Powell, 1958					
SE Australia, off New Zealand and off New Caledonia				X	
3. *M. cancellatum* G. B. Sowerby I, 1824					
Southern Japan to Philippine Islands, and Fiji Islands		X	X	X	
4. *M. exquisitum* (A. Adams & Reeve, 1848)					
Okinawa Island and southern Philippine Islands		X	X		
5. *M. grande* (A. Adams, 1855)					
Southern Japan to Philippine Islands, Indonesia, and SE Australia		X	X	X	
6. *M. joelgreenei* Emerson, 1981					
Southern Philippine Islands and Mariana Islands		X	X		
7. *M. kurzi* Petuch, 1979					
Southern Philippine Islands and Solomon Islands			X		X
8. *M. macandrewi* G. B. Sowerby III, 1889					
Southern Japan		X			
9. *M. macdonaldi* Emerson, 1981					
Marshall Islands					X
10. *M. ninomiyai* Emerson, 1986					
Off SW Thailand		X			
11. *M. praeclarum* Melvill, 1919					
Off Somali Republic, SE Africa, Mozambique, and Seychelle Islands	X				
12. *M. teramachii* Kuroda & Habe *in* Habe, 1961					
Southern Japan, Philippine Islands and Mariana Islands		X	X		
13. *M. watanabei* Kosuge, 1981					
Southern Philippines and possibly southern Japan		X	?		
14. *M. watsoni* Dance & Emerson, 1967					
Kai Islands, off New Guinea				X	
15. *M. uchiyamai* Kuroda & Habe *in* Habe, 1961					
Southern Japan, Taiwan, Mariana Islands, and New Caledonia		X	X	X	
Subgenus *Herculea* Hanley *in* H. & A. Adams, 1858					
16. *M. ponderosum* (Hanley, 1858)					
Ryukyu Archipelago, Okinawa Island, SE Australia (Queensland), New Caledonia, Tonga Islands, and Pitcairn Island			X	X	X

also occurs on the Indian-Australian Plate where it borders the Pacific Plate near the Fiji Islands. The apparent isolation of *M. ponderosum* on the southeastern Pacific Plate at Pitcairn Island could suggest a relict-faunal element, or more likely reflects larval recruitment from more westerly situated populations.

BOUCHET & POPPE (1988:24–30) discussed the biogeographical significance of the volutid genera *Alcithoe* and *Lyria* in the New Caledonian region, where *Morum bruuni* and *M. uchiyamai* are here recorded. As appears to be the case for some of the species of *Morum*, these volutes apparently also have non-planktotrophic larval development. Bouchet & Poppe concluded that the Norfolk Ridge, which

extends from New Zealand to New Caledonia, was a probable pathway for the dispersal of *Alcithoe*. In the case of *Lyria*, they presented a scenario for demersal dispersal, which seems unlikely at these depths (230–400 m), rather than one primarily based on vicariant events.

The genus *Morum* was recently allocated to the family Harpidae within a new subfamily, Moruminae (HUGHES & EMERSON, 1987; EMERSON & HUGHES, 1988). Both *Harpa* (Harpinae) and *Morum* have well-documented post-Tethyan fossil records, but *Harpa* may differ from *Morum* in the mode of development. The larvae of *Harpa*, in contrast to *Morum*, are believed to have an extended planktotrophic stage. In *Harpa*, the large capsules contain nu-

merous eggs (3000 to 4000 per capsule) and the protoconch consists of 3¼ to 5¼ whorls (HUGHES & EMERSON, 1987: 357; TAYLOR 1975:394, pl. 67; REHDER, 1973:237, pl. 208). *Harpa* is known from the Neogene of France, Italy, the Caribbean, Peru, Fiji, and Japan. Like *Morum,* most of the living species of *Harpa, i.e.,* 8 of the 10 recognized species, are largely concentrated in the Indo-Pacific biogeographical region, with one species each in tropical eastern Pacific and eastern Atlantic waters (REHDER, 1973). Unlike *Morum,* however, 50% of the Indo-Pacific species extend eastward onto the Pacific Plate. Three of the four Pacific Plate *Harpa* (*H. harpa* Linnaeus, 1758; *H. amouretta* Roeding, 1798; and *H. major* Roeding, 1798) have extensive geographical ranges, occurring from east Africa to the Hawaiian Islands, with the last two taxa also known from the Marquesas Islands (REHDER, 1973; KAY, 1979; SALVAT & RIVES, 1980). The fourth of these species (*H. gracilis* Broderip & Sowerby, 1829) may be restricted to the Pacific Plate (Ellice Islands [Vuvalu] to the Tuamotus Archipelago and Marquesas Islands [AMNH 240922], and on Clipperton Island, REHDER, 1973:243), although a specimen of this species was recently attributed to Guam, in the Mariana Islands (*teste* Albert Deynzer, 1988). It is notable that the three species of *Harpa* (*H. harpa, H. amouretta,* and *H. major*) previously reported from Guam (*teste* B. D. Smith, 1986) are also found in the Hawaiian Islands (KAY, 1979:284). The Hawaiian fauna, however, lacks *Morum* as well as representatives of the Volutidae, Cancellariidae, Turbinellidae, and other groups of prosobranch gastropods that are mostly limited to a direct developmental mode (*cf.* SCHELTEMA, 1986:253).

The sharply contrasting distributional patterns of *Morum* and *Harpa* seemingly reflect the limited biological dispersal potential of most of the species of *Morum*. With the demise of the circumtropical Tethyan seaways, *Morum* was largely restricted in the Pacific tropics to the continental margins and the larger islands off the continental borderlands. This pattern of distribution has existed despite the fact that the major current circulation in the tropical Pacific has favored east to west dispersal pathways commencing in the late Neogene or perhaps much earlier (*cf.* NEWTON, 1988), whereas the Tethyan circulation was predominately west to east (*cf.* GRIGG, 1988).

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Seasonal, Diurnal, and Nocturnal Activity Patterns of Three Species of Caribbean Intertidal Keyhole Limpets (Mollusca: Gastropoda: *Fissurella*)

by

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Abstract. The activity patterns of three intertidal keyhole limpets, *Fissurella nimbosa* (Linnaeus, 1758), *F. nodosa* (Born, 1778), and *F. barbadensis* (Gmelin, 1791), were periodically observed on Isla de Margarita, Venezuela, from November 1986 to August 1987. Two-way factorial ANOVAs indicate significant interaction among seasons and species in distances the animals moved and in the number of movements they made during their feeding excursions. *Fissurella* spp. have grazing areas of approximately the same magnitude on a seasonal basis. These congeneric fissurellids exhibited homing behavior to a scar, which was generally located near the center of the feeding range. Homing was seen most frequently in populations of *F. barbadensis* and *F. nimbosa*, and to a lesser degree in *F. nodosa*. *Fissurella nodosa* grazed diurnally 75.8% of the time; nocturnal activity patterns accounted for 61% of the grazing in *F. nimbosa* and 98.2% in *F. barbadensis*. *Fissurella nimbosa* and *F. nodosa* most commonly grazed while awash during the rising or falling tides. *Fissurella barbadensis* also fed during this time, but more typically it grazed during high tides while submerged. The temporal and spatial patterns of *Fissurella* are discussed with reference to other intertidal grazers.

INTRODUCTION

The time an animal expends obtaining food and the geographical area that it must search to collect food are two important factors in determining the ecological relationship that exists between an animal and its environment. These temporal and spatial factors are the primary elements that determine an animal's foraging behavior (HAWKINS & HARTNOLL, 1983) and help delimit the individual's home range.

The rocky intertidal coast of Isla de Margarita, Venezuela, provides excellent locations for the investigation of activity differences among congeneric herbivorous limpets of the genus *Fissurella*. PRINCZ (1973) was among the first to document the abundance of *F. nimbosa* (Linnaeus, 1758) and *F. nodosa* (Born, 1778) along this coast. Together with *F. barbadensis* (Gmelin, 1791), which is also present (PRINCZ & GONZALEZ, 1981), these archaeogastropods exhibit significant movements or activity patterns during grazing periods.

When attempting to study animal feeding, both the temporal and spatial components of activity patterns must be considered (LITTLE, 1989). Temporally, animals may feed at different times during the day or night; in intertidal animals, these times may be related to such things as the rising or falling of tides. For example, *Tectura scutum* (Rathke, 1833) grazes upslope with the incoming tide and downslope with the outgoing wash (ROGERS, 1968). In addition to tidal considerations, mollusks can partition their environment with cyclic diel activity patterns, as was reported for the prosobranch *Nerita* in Panama (LEVINGS & GARRITY, 1983). *Lottia limulata* (Carpenter, 1864) shows sensitivity to both photoperiod and tidal cycles in its activity patterns, tending to move upward during nighttime incoming tides and downward during daylight changing tides (EATON, 1968).

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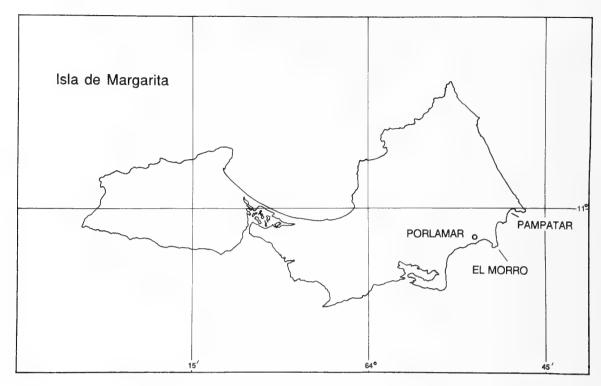
Figure 1

Map of Isla de Margarita, Venezuela, showing the locations of the two collection sites used during this study: Pampatar and El Morro.

The activity patterns of grazing animals also may have a spatial component: the animals may feed from particular locations or have regular search patterns instead of random patterns. The range of the feeding area, the placement of the animal's home scar within this range, and the magnitude of feeding excursions all provide information on how these limpets spatially utilize available resources. For example, the chitons *Acanthopleura brevispinosa* (Sowerby) and *A. gemmata* (Blainville) at low tide demonstrate temporal similarity in feeding, but spatial differences in the orientation and length of their feeding excursions (CHELAZZI *et al.*, 1983a). This permits the two co-occurring chitons to minimize zonal overlap, reducing the interspecific competition for food. Most of the members of the genus *Patella* partition their environment by occupying fixed positions on the shore, becoming established in one location and always returning to their own particular "home scar" (BRANCH, 1971). *Lottia pelta* (Rathke, 1833) exhibits spatial constraint in its feeding; it does not feed at random, but rather ingests specific alga types that are in abundance around the home site (CRAIG, 1968). An example of the complementarity of temporal and spatial aspects of activity patterns was seen in a study involving two co-occurring herbivorous neritid snails (LEVINGS & GARRITY, 1983). *Nerita funiculata* (Menke, 1851) forages from protected crevices for short times during ebbing and rising tides,

depleting algal crusts near their crevices. Unlike its congener, *N. scabricosta* (Lamarck, 1822) lives at upper tidal levels but moves down and grazes throughout the intertidal zone as the tide falls, returning as the tide rises again.

In temperate systems, dynamic physical conditions often mark the change of seasons. Air and water temperatures change, photoperiods shift with increasing darkness, and typically, tidal cycles change substantially in amplitude. In temperate climates, these physical parameters have a variability that may be used as cues to help regulate the timing and extent of feeding excursions (EATON, 1968; ROGERS, 1968). Conversely, tropical marine systems are constrained by relatively static physical conditions. For example, Isla de Margarita experiences little seasonal variability in the low-amplitude tidal flux, water and air temperatures, and day/night photoperiods. Under temperature conditions that show little seasonal variation, and in the absence of variable day-length photoperiodic cues, the tropical terrestrial prosobranch *Geophorus bothropoma* (Moellendorff, 1895) has a diurnal activity pattern (AUFFENBERG & AUFFENBERG, 1988). It is unknown whether seasonal, diurnal, or nocturnal responses exist in tropical Caribbean intertidal fissurellids as well.

Previous studies on the activity patterns of limpets frequently centered on the presence (FRANK, 1965; BREEN, 1971, 1972; RUWA & JACCARINI, 1986) or absence

(SUTHERLAND, 1970; RAO & GANAPATI, 1971; CREESE, 1980) of upshore and downshore seasonal migrations. Some earlier studies (MOORE, 1938; SOUTHWARD, 1964) attempted to relate grazing areas to animal size, but the sample sizes were small and the scope of the studies limited. No investigations have attempted to evaluate seasonal fluctuations existing in the grazing areas of limpets.

Although some information on *Fissurella barbadensis* exists concerning its feeding (WARD, 1966) and distribution in Barbados (LEWIS, 1960; WARD, 1968), the present study was conducted to provide more detailed documentation on the activity patterns of this grazer and its co-occurring congeners *F. nodosa* and *F. nimbosa*. Comparative ecological studies of the activity patterns of congeneric limpets may provide valuable insight into the manner by which these intertidal animals temporally and spatially partition their environment.

MATERIALS AND METHODS

The seasonal and diurnal activity patterns of *Fissurella nodosa, F. nimbosa,* and *F. barbadensis* were observed quarterly along the rocky intertidal zone of Isla de Margarita, Venezuela, between November 1987 and August 1988. The collection sites were El Morro (10°57.0′N, 63°49.0′W) and Pampatar (10°59.9′N, 63°47.4′W), both on the eastern coast of the island (Figure 1). These locations, which are subject to moderate wave activity, were chosen because large fissurellid populations occur there.

Vertical and horizontal quadrats were established on the rocks at the start of the study. The perimeter of these quadrats was delimited by nylon cords marked at 10-cm intervals. The corners of the quadrats were maintained by use of concrete nails driven into the rock. Limpet locations and movements were determined by measuring the horizontal and vertical coordinates of the animal. A "movement" was considered to be a change in geographical location of the limpet on the substratum over time (1 hr). Movement measurements were recorded to the nearest one-half centimeter. Fissurellids used in the studies were tagged by attaching wire markers (Thomas & Betts Corp., Raritan, NJ 08869) to the limpet shells *in situ* with a quick-drying gel acrylonitrite glue (Loctite Corp., Cleveland, OH 44128).

Observations for seasonal movements were made in the fall (November), winter (February), spring (May), and summer (August). The positions of the limpets within the quadrat were noted every hour for 24 continuous hours. Six animals of each species were observed. Distances between hourly movements were estimated by calculation of the straight-line distances between the two points. To avoid possible lunar influences on activity patterns, seasonal collections were always made within two days of a full moon.

The 24-hr coordinates of each limpet were printed graphically and grazing areas were determined by an Olympus (CUE 2) computerized image-analysis program. Because the computer scans only closed polygons, in cases

where the animals did not return to their home scar, grazing areas were artificially closed by graphical connection of the outlier with its nearest neighbor.

Limpet shell measurements were obtained by using Vernier calipers to obtain length, height, and width. The volume was determined using CUBIT's (1984) method of inverting the shells and filling them with a 50:50 ethanol : water mixture, which has less of a meniscus than pure water.

After a 24-hr observational period, the animals were detached from the rocks and preserved in 70% ethanol. During October 1987, ash-free dry weight determinations of all animals were made using a Type 1500 Thermolyne Electric Furnace (Thermolyne Sybron Corp., Dubuque, IA 52001). To avoid treatment effects due to limited furnace space, the limpets were randomized into lots of 10 each. All were processed similarly: the animals were dried for 24 hr in a drying oven at 100°C, cooled in a desiccator, weighed, dried in pre-ashed containers for 12 hr at 500°C, and finally cooled in a desiccator and weighed again. The final mass was subtracted from the dry mass of the bodies. Weights were taken to four decimal places utilizing a Mettler AC 100 balance.
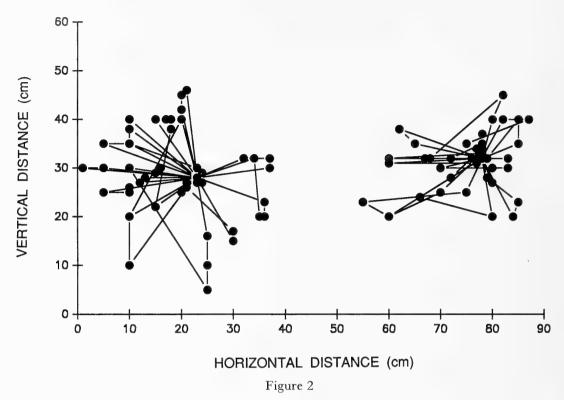
Commencing on 27 February 1987, and lasting a complete lunar cycle, the limpet movements were recorded hourly for 24 continuous hours on alternate days. Fifteen animals initially were selected for study, but during the course of the observations, three were lost to natural causes; therefore, 12 individuals were utilized in the calculations. Lunar cycles, limpet movements, times of movement, and tidal patterns were observed throughout this part of the study.

Tidal data for the observational periods were obtained from the MINISTERIO DEL AMBIENTE Y DE LOS RECURSOS NATURALES RENOVABLES (1986, 1987). Isla de Margarita experiences diurnal tidal cycles that have a daily amplitude of slightly less than one-half meter. During the study period, the greatest tidal height was recorded in December 1986 (+0.43 m) and the lowest in June 1987 (−0.13 m). Statistical analyses were performed on Systat software (Systat Inc., Evanston, IL 60202).
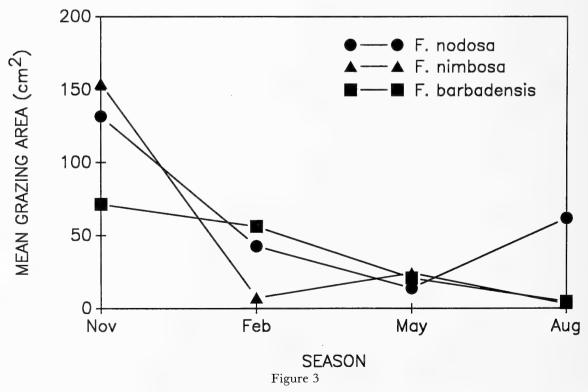
RESULTS

Seasonal and Diurnal Studies
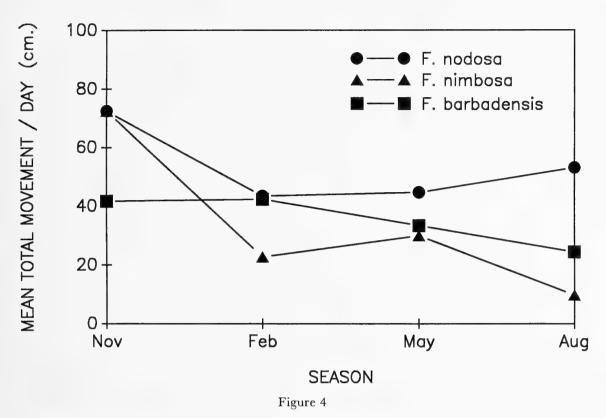
The results of the present investigation indicate that all three species of *Fissurella* return to a home scar after foraging. *Fissurella barbadensis* exhibited homing in 90% of the diurnal observations ($n = 180$). Subjective assessments (*cf.* UNDERWOOD, 1979) estimated that 80–90% of *F. nimbosa* and 30–40% of *F. nodosa* exhibit homing behavior (personal observation). Homing in limpets often results in the establishment of a distinctive rock scar into which the contours of the limpet shell fit with great precision. In *Fissurella,* the tightly fitting home scar is usually located in the center of the foraging area (Figure 2) around which

Figure 2

Activity patterns of two individuals of *Fissurella barbadensis* at El Morro, Isla de Margarita, Venezuela, during 13 days and nights in March 1987. Dots represent the actual coordinates of the limpets on a vertical rock surface during hourly observations. Axes indicate vertical and horizontal coordinates during observation intervals.

Figure 3

Seasonal differences of three *Fissurella* spp. in their mean grazing areas (GA).

Figure 4

Seasonal differences of three *Fissurella* spp. in the mean length of total movements (TM) on vertical surfaces during 24-hr observation periods.
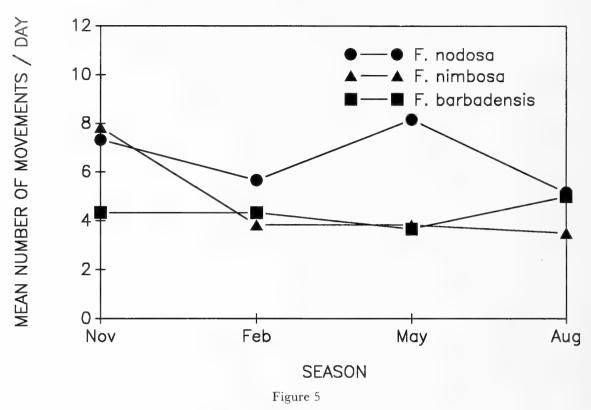
feeding takes place in a 360° arc. When they return to the home scar, fissurellids position themselves exactly as oriented prior to departure. There were no tendencies among the three species of fissurellids to establish a home scar orientation (up, down, east, west, etc.) ($\chi^2 = 1.57$, $n = 114$).

Analysis of the limpet grazing areas (GA) indicates that significant seasonal effects exist (2-way ANOVA, d.f. = 60, $P = 0.001$) (Figure 3). Although all three species of *Fissurella* had their largest GA values during the fall season and their lowest during the spring, significant differences were found neither among species ($P = 0.398$) nor in the interactions between species and seasons ($P = 0.172$). Accordingly, *F. nimbosa, F. nodosa,* and *F. barbadensis* all can be assumed to have grazing areas of approximately the same magnitude.

Analyses of the total movement (TM) distances of animals during 24-hr intervals indicate that, regardless of season, *Fissurella nodosa* consistently has greater TM than *F. barbadensis* or *F. nimbosa* (Figure 4). Season (2-way ANOVA, d.f. = 60, $P = 0.001$), species ($P = 0.002$), and interaction ($P = 0.029$) effects are significant for TM: the distance moved depends on both the species and season. Linear contrasts fail to discriminate between *F. nimbosa* and *F. barbadensis*, indicating that *F. nodosa* has different TM values than the other species. Whereas mean values

for TM of *F. nimbosa* and *F. barbadensis* are similar, a high variance is found for *F. nimbosa* because occasionally no movement is found during a given 24-hr period; at other times, there may be relatively long feeding excursions. This phenomenon for *F. nimbosa* has been reported elsewhere (FRANZ, in press a).

An analysis of the number of movements (NM) an animal makes per diel cycle indicates significant species (2-way ANOVA, d.f. = 60, $P = 0.001$), season ($P = 0.022$), and interaction ($P = 0.016$) effects (Figure 5). The overall average of movements for *Fissurella nodosa* (6.6 movements/24 hr) was greater than the other species; except in the fall, *F. nodosa* seasonally averaged a greater number of movements per day than the other limpets. Its excursions varied from a greater NM during the fall and spring to a lower NM during winter and summer. Even with a high fall value for movement by *F. nimbosa*, there was no difference in the mean NM between this limpet and *F. barbadensis*; both *F. nimbosa* and *F. barbadensis* averaged approximately 4.5 movements per 24-hr period. Because measurements were taken at hourly intervals and realizing that these animals feed primarily while moving, these measurements of movement may additionally reflect the number of hours the animals graze on a daily basis. However, these animals may occasionally feed while not moving and this measurement is most likely an underestimate of feed-

Figure 5

Seasonal differences of three *Fissurella* spp. in the mean number of movements (NM) on vertical surfaces during 24-hr observation periods.

ing time. Rarely have I observed them moving without foraging.
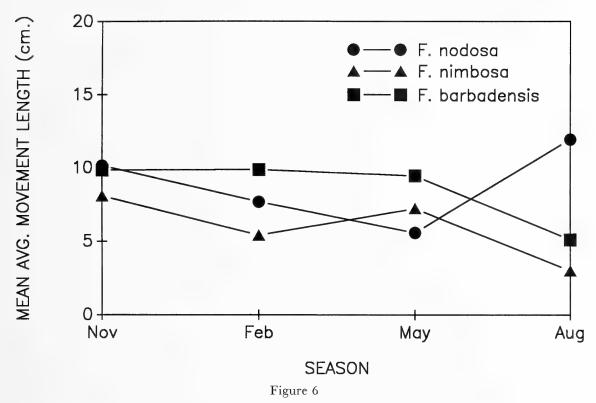
Investigations of the average movement lengths (ML) of a given limpet during a feeding excursion, determined by dividing the sum of the lengths by the number of movements, yielded no significant differences between the seasons (2-way ANOVA, d.f. = 60, $P = 0.082$). Differences among the fissurellid species ($P = 0.003$) and interactions ($P = 0.001$) indicate that ML depends on both species and season (Figure 6). The relatively consistent seasonal trends for average movement lengths among all three *Fissurella* showed a marked decline in their summer values. The mean values for *F. nodosa, F. nimbosa,* and *F. barbadensis* were 8.84 cm, 5.93 cm, and 8.58 cm, respectively; linear contrasts failed to separate the average movement length of *F. nodosa* from those of *F. barbadensis.* The interaction effect is most probably due to the differences in spring and summer movements; for all three species, tests for the difference between means during these months were significant at the $P = 0.05$ level.

Individuals of *Fissurella* may travel great distances in their feeding excursions. Maximal hourly movements of 57 cm were witnessed for *F. nodosa,* while both *F. barbadensis* and *F. nimbosa* moved as far as 26 cm in an hour.

An analysis of the physical characteristics of each species was conducted. This analysis included measurements of length, width, height, volume of the shell, dry weight of the animal, and ash-free dry weight of the animal. In the present study of intertidal archaeogastropods, these variables showed relatively high Pearson correlation values (Table 1). The dry weights and ash-free dry weights were strongly correlated ($r = 0.994$). These physical dimensions were uncorrelated with grazing area, however.

Among the three species of *Fissurella,* there was temporal partitioning of grazing excursions. A total of over 240 daily observations were made of individual fissurellids during which time a total of 1136 movements were recorded. After separation of data by species, the data were subdivided into two groups depending upon whether the grazing activity occurred during the day (0700 to 1800 hr) or night (1900 to 0600 hr). Thirty-nine percent of the feeding excursions for *F. nimbosa* occurred during daylight hours while *F. nodosa* did 76% of its feeding during that time. For both species, there was no difference in the average distance a limpet moved during its feeding excursions when diurnal and nocturnal values were compared. Additionally, both species fed most intensely during periods of rising tides (Table 2). *Fissurella barbadensis* was primarily a nocturnal grazer: 98.7% of the movements of this animal occurred during the night interval between 1900 and 0600 hr.

Fissurella exhibited no apparent pattern to the direction

SEASON

Figure 6

Seasonal differences of three *Fissurella* spp. in the mean movement length (ML) on vertical surfaces during 24-hr observation periods.

in which foraging occurred after leaving the home scar. The limpets were as likely to move upward as downward, or to the right as to the left; on subsequent nights, feeding excursions would be in different directions. Although CONNOR (1986) reported that the homing limpets *Lottia gigantea* and *Collisella scabra* capitalize on their food-en-

hancing mucus by retracing their trails, *F. barbadensis* exhibited little iteration over a given trail during a month of observed activity. There was no evidence of increased macrophytic growth on fissurellid trails.

Nocturnal Studies

Fissurella barbadensis was used to study the effects of lunar cycles on limpet feeding behaviors. This species was chosen because it is almost exclusively nocturnal and has

Table 1

Pearson correlation matrix of body dimension data and grazing areas for *Fissurella* spp. (n = 72 individuals) collected from Isla de Margarita, Venezuela during 1986 and 1987. Abbreviations are for shell length (LGTH), shell width (WDTH), shell height (HGTH), shell volume (VOL), animal dry weight (DRYWT), ash-free dry weight (ASHWT), and grazing area (AREA).

	LGTH	WDTH	HGTH	VOL	DRY WT	ASH WT	AREA
LGTH	1.000						
WDTH	0.969	1.000					
HGTH	0.858	0.862	1.000				
VOL	0.947	0.936	0.879	1.000			
DRYWT	0.865	0.863	0.884	0.924	1.000		
ASHWT	0.873	0.868	0.900	0.931	0.994	1.000	
AREA	0.151	0.144	0.163	0.184	0.063	0.080	1.000

Table 2

Percentage of feeding excursions of *Fissurella* on Isla de Margarita, Venezuela, during different aspects of the tidal cycle. Data were collected between November 1986 and August 1987; the movements were recorded hourly for complete tidal cycles. The total number of movements, from which these percentages are derived, are listed in parentheses.

Species		Tidal condition			
		High	Falling	Low	Rising
F. nodosa	(n = 210)	0.148	0.224	0.133	0.495
F. nimbosa	(n = 126)	0.119	0.270	0.175	0.436
F. barbadensis	(n = 146)	0.528	0.207	0.007	0.257

a clearly discernible home scar. Although the shell of these limpets may be covered with algal growth and blend into the environment well, an animal's absence from its home scar is easily recognizable. During the 13-hr period from 1900 to 0700 hr, *F. barbadensis* was active for an average of 4.5 hr. Generally speaking, these animals grazed most actively between midnight and 0500 hr; of the movements observed during the one-month sample period, 70.2% of them occurred during these hours. Among individuals of *F. barbadensis,* a trend was apparent towards more intense grazing activity at later hours during a new moon and earlier hours during an old moon. During a full moon, the limpets had intermediate feeding times between 1900 and 0600 hr.

DISCUSSION

The extent to which animals establish grazing areas around their home scar is dependent upon a number of interrelated variables: locomotory rate, turning angles, frequency of turns, stops, lengths of straight components, total path length, randomness or straightness, and end-point location (SINIFF & JESSEN, 1969). The interrelation of these spatial variables is particularly relevant in the activity patterns of intertidal fissurellids. *Fissurella nimbosa* and *F. barbadensis* have approximately the same number of movements, length of movements, total distance travelled, and grazing area. Contrarily, *F. nodosa* exhibits greater movement lengths and number of moves, yet its grazing area is the same as the other congeners studied. Amid these diverse combinations of geometric parameters, it is enigmatic why the seasonal grazing areas of *Fissurella* spp. are similar and why interactional effects are absent. Among other activity patterns, 2-way ANOVAs for TM, NM, and ML indicate the presence of interactions. Obviously, a complex spatial relationship exists among movement variables in fissurellid activity patterns. I suspect that differential foraging techniques (FRANZ, in press a) and unique food preferences (FRANZ, in press b) may influence fissurellid activity patterns.

Temporal conditions also influence activity patterns. Similar to the limpet *Collisella scabra* (Gould, 1846), *Fissurella nodosa* feeds during the day. *Fissurella nimbosa* feeds both during the day and at night as do *Cellana toreuma* (Reeve, 1855) (HIRANO, 1979), *Lottia limulata* (WELLS, 1980), *Tectura scutum* (Rathke, 1833) (ROGERS, 1968), *Siphonaria normalis* (Cook, 1969), *S. alternata* (Say, 1822) (COOK, 1971), and *S. pectinata* (Linnaeus, 1758) (THOMAS, 1973). An earlier investigation conducted on Barbados reported that *F. barbadensis* fed periodically throughout the night and day (WARD, 1966); however, the present study indicates that *F. barbadensis* is almost exclusively a nocturnal feeder. Such activity may minimize visual identification by predators (*cf.* LEVINGS *et al.,* 1986), although this hypothesis was not tested.

A number of mollusks (BRANCH, 1981; HAWKINS & HARTNOLL, 1983; LITTLE, 1989) and crustaceans (JANDER,

1975; VERNBERG & VERNBERG, 1983) have tide-influenced grazing patterns. *Fissurella nodosa* and *F. nimbosa* show the greatest feeding activity when awash during rising or falling tides; *F. barbadensis* feeds principally while submerged. Such behavior may be due to differential desiccation tolerance among the congeners.

Homing is a well-established phenomenon in many genera of limpets including *Siphonaria* (COOK, 1969, 1971; COOK & COOK, 1975), *Patella* (BRANCH, 1971), *Collisella* (JESSEE, 1968), *Lottia* (STIMSON, 1970), *Cellana* (UNDERWOOD, 1977), and *Fissurella* (WARD, 1966). Homing behavior has been observed in chitons such as *Liolophura* (NISHIHAMA *et al.,* 1986), *Sypharochiton* (KNOX, 1963), *Acanthopleura* (CHELAZZI *et al.,* 1983b), and *Acanthozostera* (THORNE, 1968). Among the congeneric limpets studied here, homing was more strongly exhibited by some species than others: *F. barbadensis* > *F. nimbosa* > *F. nodosa.*

The selective advantage of homing is uncertain; however, this behavior may serve to avoid predation (PHILLIPS & CASTORI, 1982; GARRITY & LEVINGS, 1983; KUNZ & CONNOR, 1986) and optimize algal resources (HAWKINS & HARTNOLL, 1983). Hence, the location of a fissurellid home in the center of the foraging area may provide protection and an efficient initiation point for subsequent excursions. Other researchers have suggested that homing may minimize desiccation (VERMEIJ, 1973; BRANCH, 1981; VERDERBER *et al.,* 1983; GARRITY, 1984), but this would make sense only for species that live high on the intertidal zone. Because *Fissurella* exhibits an inverse relationship between homing and intertidal height of the home scar, the avoidance of desiccation is unlikely to be the primary explanation for homing in these limpets.

UNDERWOOD (1979) suggested that homing behavior maintains a pattern of density dependent distribution which leads to even dispersal of the population. Subsequently, maximal utilization of food resources can be achieved by partitioning the available food supplies. Indeed, density dependent assemblages of *Fissurella virescens* Sowerby have been reported along the Pacific coast of Costa Rica (ORTEGA, 1985). Although the present study was not designed to examine competitive relationships among species, data collected from the lunar study indicate that *F. barbadensis* forms grazing territories. Where two individuals are neighboring, there appears to be spatial partitioning of the available food resources by establishment of discrete home ranges (Figure 7). Although some overlap of foraging areas occurred, the grazing area boundaries of an individual limpet were generally well respected. Other limpets such as *Lottia gigantea* Sowerby, 1834 (STIMSON, 1970, 1973) and *Patella longicosta* (Lamarck) (BRANCH, 1975b) defend their territories rigorously, but this was never observed for *Fissurella.*

Unlike other species such as *Lottia digitalis* (Rathke, 1833) (MILLER, 1968) and *L. gigantea* (ABBOTT, 1956) which orient with their head facing downward on vertical or nearly vertical rocks, there were no tendencies among
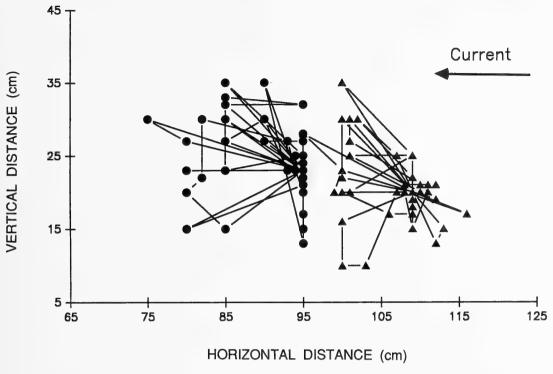
Figure 7

Movement patterns of two individuals of *Fissurella barbadensis* at El Morro, Isla de Margarita, Venezuela, during 13 days and nights in March 1987. Dots and triangles represent the actual location of the two limpets on a vertical rock surface during hourly observations. A persistent and very strong current probably caused the noticeably asymmetric grazing pattern.

Fissurella spp. to orient in a particular direction when on their home scar. COLLINS (1976) reported that in *Collisella scabra* the inclination angle of the substratum may influence the potential for desiccation and this topographical feature may influence distributional patterns. In the present study, *F. nodosa* and *F. nimbosa* were almost always located on a vertical wall, frequently homing close to algal tufts that provided shading during low tide periods and protection from impacting waves. *Fissurella barbadensis* was found typically on flat, subtidal rock platforms.

Studies on prosobranch limpets (BRANCH, 1975a; BRETOS, 1982) have indicated that high correlations may exist among such characters as height, length, width, volume, dry weight, and ash-free dry weight. Indeed, among these characters, strong relationships were found for *Fissurella nodosa, F. nimbosa,* and *F. barbadensis*. Although significant statistical relationships have been found between body size and grazing areas in terrestrial mammals (SWIHART *et al.,* 1988) and between shell length and grazing distances for Japanese limpets (HIRANO, 1979), such relationships were not found among *Fissurella*. Failure to find a significant linear association between animal size and grazing distances has been reported by COOK & COOK (1981) for *Siphonaria* limpet populations.

Although the congeneric variations noted above would

tend to suggest micro-partitioning of the environment on both spatial and temporal scales, additional experiments involving manipulations of limpet densities together with exclusion and replacement studies are needed to fully evaluate the impact that variable activity patterns have on fissurellid co-occurrence along the Venezuelan intertidal zone.

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Anatomy of the Circulatory System of the Nudibranch *Platydoris argo* (Linné, 1767) with Comparisons among Doridacea (Gastropoda: Opisthobranchia)

by

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Abstract. The anatomy of the circulatory system of *Platydoris argo* (Linné, 1767) is described. The morphology of the heart and the placement of its valves are studied in detail. The auriculoventricular and aortic valves may prevent a backward blood flow. Blood coming from the branchial ring enters the auricle through the caudomedial opening, while the blood that comes from the lateral sinuses goes into the auricle through the lateral openings. The distribution of the arterial system throughout the animal's body is described. Following this, the variability of the circulatory system in Doridacea is compared and discussed, showing the changes in the heart, gills, and main blood vessels within the suborder.

INTRODUCTION

The circulatory system of the Nudibranchia has been studied little. Detailed studies on Doridacea are few, even though they have varied anatomical features (POTTS, 1981; WÄGELE, 1984; JONAS, 1985). Thus, the gills of dorids can be located on the notum or around the anus, or they can be disposed along both sides between the notum and the foot. In addition, the stage of complexity in the development of the gills differs within the suborder. The range of forms includes some leaflets or simply pinnate gills, not retractile, as well as complex tripinnate gills retractile within a branchial pocket. According to variations of the respiratory structures, the vascular system also shows modifications in the afferent and efferent branchial vessels.

The present work describes in detail the circulatory system of a cryptobranchiate dorid and compares it to that of other doridacean mollusks.

MATERIALS AND METHODS

The seven specimens of *Platydoris argo* (Linné, 1767) used for this study were collected in the Strait of Gibraltar (southern Spain) and measured between 6 and 10 cm in length. Four of these animals, collected in August 1985, had been preserved in 4–5% formalin. The other three specimens, obtained in October 1988, were anesthetized with magnesium chloride before preservation in formalin, in order to keep their gills extended for anatomical investigations.
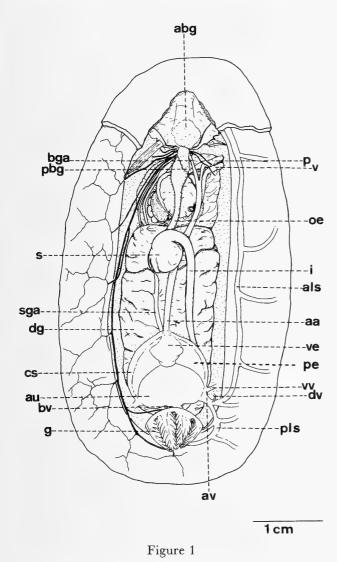
Dissections were made with fine forceps and needles using a stereomicroscope. Details of vessels and sinuses were observed by sectioning the notum of the specimens that were preserved in formalin and staining them with methylene blue. In the anesthetized specimens, a bubble of air was injected into the ventricle and main arteries, allowing us to follow the blood stream throughout the body.

RESULTS

Pericardium

The pericardium is a spacious cavity lying posteriorly on the digestive gland in front of the branchial circle (Figure 1). Associated with the pericardial cavity are the following vessels: (*a*) the aortic trunk (Figure 3, at), which is the beginning of the arterial system and is located just anterior to the pericardium; (*b*) the branchiocardiac vein (bv), which is located at the posterior extreme of the pericardium and connects the afferent branchial ring to the auricle; and (*c*) the auricular veins (av), which connect the lateral sinuses to the side of the auricle. The circular sinus

1 cm

Figure 1
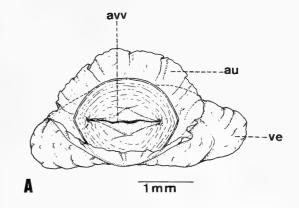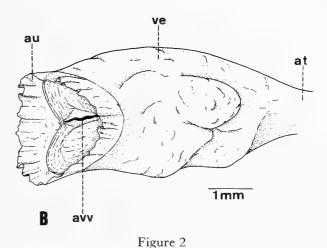
Dorsal view of a dissected *Platydoris argo*. aa, anterior artery; abg, anterior blood gland; als, anterior lateral sinus; au, auricle; av, auricular vein; bga, blood gland artery; bv, branchiocardiac vein; cs, circular sinus; dg, digestive gland; dv, dorsal vein; g, gill; i, intestine; oe, oesophagus; p, penis; pbg, posterior blood gland; pe, pericardium; pls, posterior lateral sinus; s, stomach; sga, superior gastric artery; v, vagina; ve, ventricle; vv, ventral vein.

1 mm

Figure 2

Posterior (A) and lateral (B) view of the ventricle of *Platydoris argo*. at, aortic trunk; au, auricle; avv, auriculoventricular valve; ve, ventricle.

(cs) is a spacious inner cavity that encircles all but the posterior end of the pericardium. The only connection between this sinus and other structures is through the auricular vein, which connects to the auricle.

The heart lies within the pericardial cavity and has a rhomboid-shaped muscular ventricle and a thin-walled, globular-shaped auricle. Blood flows from the gills to the auricle through the branchiocardiac vein. The auricle also receives blood through the lateral auricular veins from a plexus of sinuses. These sinuses, which extend throughout the notum, are the sites of cutaneus respiration.

There are two valves in the heart: the auriculoventricu-

lar valve (Figure 2, avv) that has two flaps projecting into the cavity of the ventricle from the auricle, and the aortic valve (Figure 3, aov) that has a ventral flap between the ventricle and the aortic trunk.

Peripheral Circulation

The peripheral circulation (Figure 1) consists of a plexus of sinuses that extend throughout the notum and foot of the animal. These sinuses drain laterally into two pairs of longitudinal sinuses—the anterior (als) and posterior lateral sinuses (pls)—located along the sides of the body. The anterior lateral sinus extends longitudinally up to the posterior lateral extreme of the pericardial cavity, receiving blood mainly from the lateral notum and draining it into the auricular veins. The posterior lateral sinus extends from the posterior extreme of the animal to the pericardial cavity; it carries blood from the portion of the notum located behind the pericardium and the auricular veins. The auricular veins receive blood from the dorsal notum sinuses

Figure 3

Dorsal view of the gonohepatic mass and stomach of *Platydoris argo* to show the arterial and venous systems. aa, anterior artery; abr, afferent branchial ring; aov, aortic valve; at, aortic trunk; dg, digestive gland; fga, female gland artery; i, intestine; ms, medial sinus; oe, oesophagus; pe, pericardium; pta, prostatic artery; rch, renal chamber; rv, renal vesicle; s, stomach; sga, superior gastric artery; (1), artery to prostate and female gland.

Figure 4

Partial lateral view of the branchial vessels and the afferent and efferent rings of *Platydoris argo*. abr, afferent branchial ring; abv, afferent branchial vessel; bn, branchial nerves; ebr, efferent branchial ring; ebv, efferent branchial vessel; grm, gill retractor muscle.

through the dorsal vein (dv). Blood flows from the ventral sinuses to the circular sinus through the ventral vein (vv).

Branchial Circulation

Blood from the visceral organs is drained into a common medial sinus (Figure 3, ms) that extends along the digestive gland and under the pericardium. This sinus connects posteriorly to the afferent branchial ring (abr), which lies beneath the branchial tuft that partially encircles the anal and renal orifices. Blood passes from the afferent branchial ring into the afferent branchial vessels (Figure 4, abv), which extend longitudinally along the inner edges of the gills. These veins ramify into several small vessels that

extend into the gill pinnules. Blood passes from the afferent branchial vessels to the efferent branchial vessels (ebv). These lie on the outer surface of the gills and join the efferent branchial ring (ebr), which lies ventral to the gill tuft and encircles the afferent branchial ring. The efferent
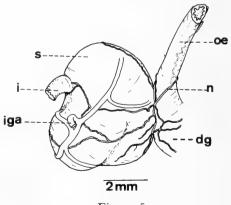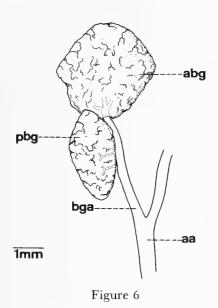
Figure 5

Ventral view of the stomach of *Platydoris argo*. dg, digestive gland; i, intestine; iga, inferior gastric artery; n, nerves; oe, oesophagus; s, stomach.

Figure 6

Blood gland of *Platydoris argo*. aa, anterior artery; abg, anterior blood gland; bga, blood gland artery; pbg, posterior blood gland.
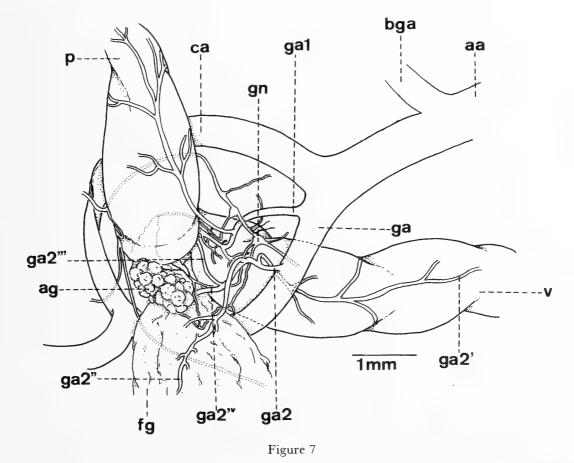
branchial ring connects anteriorly with the auricle through the branchiocardiac vein.

Both the afferent and efferent branchial ring are horse-shoe-shaped.
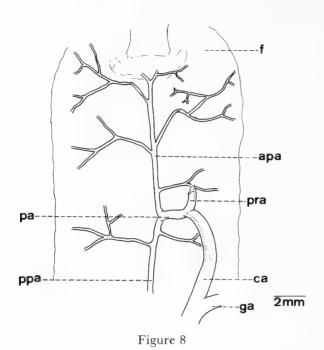
Arterial Circulation

The ventricle lies posterior to a large aortic trunk from which several vessels branch off toward different organs.

The anterior artery (Figure 3, aa) branches anteriorly from the anterior extreme of the aortic trunk (at). At the level of the stomach the inferior gastric artery (Figure 5, iga) branches off and underlies the ventral surface of the stomach. On the right side, at the same level, a branch from the anterior artery passes into the right part of the digestive gland (Figure 3). The anterior artery continues forward, and at the level of the reproductive organs bifurcates, the right branch continuing forward, while the left one passes into the blood glands (blood gland artery, Figure 1, bga). Two small lateral branches connect with the posterior blood gland and then branch throughout that gland. Connections with the anterior blood gland are made

Figure 7

Superior view of the distal part of the genital system of *Platydoris argo*. aa, anterior artery; ag, annex gland; bga, blood gland artery; ca, cephalic artery; fg, female gland; ga, ga1, ga2, ga2′–ga2^{IV}, genital arteries; gn, genital nerves; p, penis; v, vagina.

Figure 8

Arterial vessels of the foot of *Platydoris argo*. apa, anterior pedal artery; ca, cephalic artery; f, foot; ga, genital artery; pa, pedal artery; ppa, posterior pedal artery; pra, probuccal artery.

Figure 9

Arterial vessels of the buccal mass (ventral view) of *Platydoris argo*. ba, buccal artery; br, buccal retractor muscle; bs, buccal sinus; m, mouth; oa, oral artery; ot, oral tube; pra, probuccal artery; rs, radular sac; vd, ventrolateral dilator muscle.
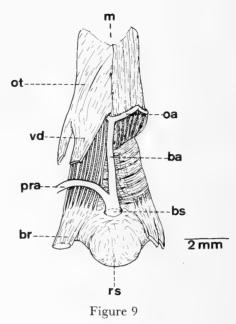
through the posterior extreme of the blood gland artery (Figure 6, bga).

The right branch of the anterior artery continues forward and bifurcates again. One branch, the genital artery (Figure 7, ga), extends to the ventral surface of the reproductive organs between the penial and vaginal sheaths; the other, the cephalic artery (ca), continues toward the cephalic region.

The genital artery penetrates the reproductive organs and gives rise to several blood vessels (Figure 7, designated ga1 and subdivisions of ga2). Near the common genital atrium, a side branch of the ga1 extends longitudinally along the penial sac and ramifies. The ga2 gives off several branches to the vagina and outer oviduct (ga2′), female glandular mass (ga2″), common genital atrium (ga2‴) and vestibular gland (ga2^{IV}). The genital artery (ga) continues to the female glandular mass.

The cephalic artery (ca) surrounds the penial sac up to the ventral surface of the body and bifurcates; one branch goes to the foot (Figure 8, pedal artery, pa) and the other goes to the buccal apparatus (probuccal artery, pra). The former bifurcates and gives off one branch forward (anterior pedal artery, apa) and another backward (posterior pedal artery, ppa); both vessels are highly ramified.

The probuccal artery enters directly into the buccal apparatus between the buccal retractor muscles (Figure 9, br) and drains into the buccal and odontophoral sinuses. The buccal artery (Figure 9, ba) branches off of the probuccal artery just before it contacts the buccal apparatus.

The buccal artery extends forward to the posterior extreme of the oral tube and bifurcates (oral arteries, Figure 9, oa), one branch running to the right and the other to the left on the oral tube (Figure 10).

The superior gastric artery (Figure 3, sga) arises from the aortic trunk, to the left of the anterior artery, and branches of the superior gastric artery supply the oesophagus, stomach, gonad, and digestive gland. Additional blood vessels also supply the gonad, digestive gland, and renal chamber. One of these vessels runs forward and bifurcates (1). The left branch, the prostatic artery, passes to the posterior extreme of the prostate and enters it (pta); the right branch bifurcates, with the two branches passing within the albumen and mucous gland respectively (fga).

Venous Circulation

Overlying the digestive gland is a large longitudinal sinus (or medial sinus; Figure 3, ms) that receives blood from the veins of the various organs. From the medial sinus blood passes to the afferent branchial ring.

DISCUSSION

From these detailed observations of *Platydoris argo* the direction of blood flow has been interpreted as follows. Blood from the arterial circulation passes to the pedal arteries and sinuses, which probably contributes to the overall turgor of the foot and provides nutrients and oxygen to the tissues (VOLTZOW, 1985, 1986). From the foot, blood passes to the plexus of sinuses in the notum, which connects
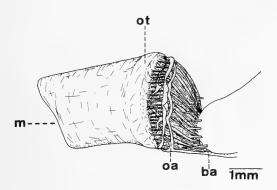
Figure 10
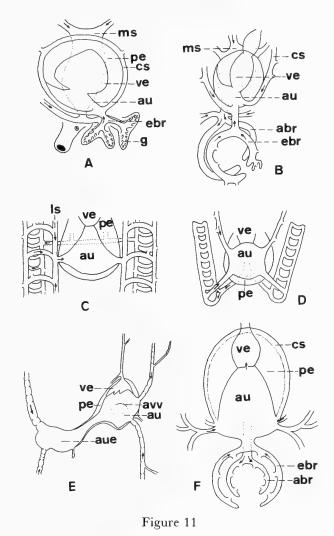
Disposition of the oral artery (lateral view) of *Platydoris argo*. ba, buccal artery; m, mouth; oa, oral artery; ot, oral tube.

Figure 11

Diagrammatic reconstruction of the venous and branchial regions of Doridacea. A, *Bathydoris obliquata*; B, *B. vitjazi*; C, *Phyllidia pulitzeri*; D, *Corambe*; E, *Doridoeides gardineri*; F, *Platydoris argo* (A and B, after MINICHEV, 1970; C, after WÄGELE, 1984; D, after WÄGELE, 1984, based on FISCHER, 1892; E, after ELIOT & EVANS, 1908). The arrows represent the direction of blood flow. abr, afferent branchial ring; au, auricle; avv, auriculoventricular valve; cs, circular sinus; ebr, efferent branchial ring; g, gill; ls, lateral sinus; ms, medial sinus; pe, pericardium; ve, ventricle.

to the lateral sinuses. These sinuses drain blood into the auricle through the auricular veins. From the visceral mass, blood flows into the medial sinus and passes backward to the afferent branchial vessels. A similar interpretation was given by HANCOCK & EMBLETON (1852) and ELIOT (1910) for several species of *Doris* and for *Doris tuberculata* Müller, 1778, respectively.

The circulatory system of *Platydoris argo* differs in several ways from that of *Doris* as described by HANCOCK & EMBLETON (1852): (a) the superior gastric artery is independent in *P. argo* (the gastric artery of HANCOCK & EMBLETON [1852] is the inferior artery in *P. argo*); (b) there are only a few connections between the circulatory and excretory systems of *P. argo*, but *Doris* appears to have many; (c) the afferent and efferent branchial rings are horseshoe-shaped in *P. argo*, whereas the rings are closed in *Doris*. ELIOT (1910) found that in *Doris tuberculata* (=*Archidoris tuberculata*) the efferent branchial ring is closed and the afferent branchial vessels are horseshoe-shaped. On the other hand, *Onchidoris bilamellata* Linné, 1767, and *Archidoris pseudoargus* (Rapp, 1827) (see POTTS, 1981) and *Peltodoris atromaculata* Bergh, 1880 (see JONAS, 1985) appear to have afferent and efferent branchial rings similar to those described here for *P. argo*.

The buccal mass circulation of *Platydoris argo* differs fundamentally from that of *Onchidoris bilamellata*, which has been excellently described by CRAMPTON (1977): in *P. argo*, (a) the pedal artery bifurcates into an anterior branch (the anterior pedal artery) and a posterior branch (the posterior pedal artery), both of which extend to the central area of the body; (b) there is only one central buccal artery, which bifurcates into two oral arteries. According to CRAMPTON (1977) in *O. bilamellata* there are two lateral pedal arteries on the right and left side respectively and two buccal arteries.

The circular sinus described in *Platydoris argo* has been noted before in only a few doridaceans: by EVANS (1914) in *Bathydoris browni* Evans, 1914, by MARCUS & MARCUS (1962) in *B. aioca* Marcus & Marcus, 1962, and by MINICHEV (1970) in *B. browni*, *B. obliquata* Odhner, 1934,

and *B. vitjazi* Minichev, 1969. However, in these species the circular sinus opens to the plexus of sinuses from the peripheral circulation, before connecting to the auricle (Figure 11A, B). We have not seen such openings in *P. argo*. On the other hand, in the most primitive species of the genus *Bathydoris* (*i.e.*, *B. browni*, *B. obliquata*), the circular sinus surrounds the pericardium (Figure 11A), whereas in higher species (*i.e.*, *B. vitjazi*), the circular sinus has a tendency to become separated from the pericardium to form the lateral sinuses that are present in the majority of Doridacea (Figure 11B). Thus, in *P. argo*, which has well-differentiated lateral sinuses, the circular sinus could

be a relic structure homologous to that of the primitive doridaceans and the pleurobranchids, in which, as stated by LACAZE-DUTHIERS (1859), EVANS (1914), and MARCUS & MARCUS (1962), the circular sinus collects the blood returning from the skin to the auricle.

At the same time in evolution as the lateral sinuses are differentiated, the organization of the typical dorsal and perianal corolla of gills is produced and the heart is modified.

The gills of Doridacea have been considered as a primary gill or ctenidium (that is, homologous to those of the shelled forms) according to their innervation, the position of the gills relative to the anus and renal orifice, embryological development, and the occurrence of a raphe (EVANS, 1914; MINICHEV, 1970; TARDY, 1970; JONAS, 1985). As such the gill of the Doridacea originates directly from that of the Notaspidea, which is placed asymmetrically on the right side. This asymmetry is present in the primitive doridaceans (Bathydorididae). In more advanced dorids the gills are situated dorsally in the midline on the notum. The heart shows similar changes, as it changes from an asymmetrical to a central position in the Doridacea. Further, two kinds of entrance of blood into the auricle are differentiated: posteriorly the blood flows from the gills and laterally it passes from the lateral sinuses.

As is illustrated in Figure 11A, *Bathydoris obliquata* has the heart placed asymmetrically on the right side and has only a common entrance of blood from the gills and circular sinus to the auricle. MINICHEV (1970) states that in *B. vitjazi* an intermediate situation exists in which the right part of the circular sinus opens independently into the auricle (see Figure 11B). Finally, the gills and heart of higher doridaceans are situated in the midline and the two afferent systems of the auricle are well differentiated.

In Corambidae the organization of the gills and the heart is different from that of the rest of Doridacea. In this family the gills are located posteriorly between the notum and foot and the auricle has two lateral posterior entrances of blood from the gills and two lateral anterior ones from the lateral sinuses (Figure 11C).

The differences between the branchial and circulatory systems in doridacean species, with dorsal gills (*i.e., Platydoris argo*), and species of Phyllidiidae, in which the gills are located along both sides between the notum and the foot, were show by WÄGELE (1984). Wägele noted that the gills of Phyllidiidae are not homologous to the ctenidium but rather are secondary gills; furthermore, the caudomedial entrance of blood into the auricle is not present, so that in *Phyllidia pulitzeri* Pruvot-Fol, 1962, the lateral sinuses return the blood to the auricle from the sites of cutaneous respiration and from the gills. Some of the gillless doridaceans (*i.e., Doridoeides gardineri* Eliot & Evans, 1908) do not have the caudomedial entrance either (see Figure 11E).

It is necessary to compare the gills of the Corambidae and Phyllidiidae to determine whether they are homologous with each other and to demonstrate whether the or-

ganization of the gills of Corambidae constitutes an intermediate situation between the typical organization of Doridacea and phyllidiids.

According to BABA (1937), in *Okadaia elegans* Baba, 1931, one cannot easily determine which of the two chambers is the ventricle and which is the auricle, because the heart is not connected to any blood vessel and both chambers are thin walled. Furthermore, the heart is not enclosed within a pericardium. BABA (1937) states that the function of this peculiar heart could be the maintenance in the hemocoel of a current blood that is oxygenated by cutaneous respiration. POTTS (1983) suggests that in smaller dorids the dorsal notum appears to be the main site of gaseous exchange, whereas in large animals the gills provide the main respiratory structure. On the other hand, ELIOT & EVANS (1908) noticed that in doridaceans in which respiration occurs over the entire external surface, as opposed to in a special organ, a strong heart and an extended arterial system are not necessary. These data could explain the organization in *Okadaia elegans,* because it is a small (less than 5 mm in length) gill-less dorid with only cutaneous respiration. A similar situation was noted by GRAHAM (1982) about the prosobranch *Cima minima* (Jeffreys, 1858); because of its small size (less than 1.5 mm), the surface area to volume ratio is so large that neither gill nor heart is necessary.

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The Malacological Contributions of
Ida Shepard Oldroyd and Tom Shaw Oldroyd

by

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Abstract. Tom Shaw Oldroyd (1853–1932) and Ida Shepard Oldroyd (1856–1940) amassed a large private collection of mollusks. During their lifetimes, this material was incorporated into the Stanford University collections, which eventually became part of the holdings of the California Academy of Sciences. Altogether, the Oldroyds proposed 59 new species-group names, as follows: 10 for bivalves, including 3 *nomina nuda,* the rest now regarded as synonyms; 47 for gastropods, including 2 *nomina nuda,* 23 synonyms, 4 valid, and 18 of uncertain status, mostly pyramidellids; one that is a probable synonym in the Annelida; and one for a stony coral. Type material has been located and documented for all but one of the nomenclaturally available taxa.

Tom Shaw Oldroyd was born in Huddersfield, England, 13 June 1853, and two years later his family moved to Flushing, New York. He moved to California in 1880, living first in Los Angeles, then in Long Beach, earning a living as a handyman. Here he began collecting shells (ANON., 1932, 1933)[1].

Ida Shepard was born in Goshen, Indiana, 25 November 1856. After attending high school in Saline, Michigan, she received a teaching certificate from the University of Michigan. In 1888, her family moved to Long Beach, where she too began making a shell collection (CHACE, 1940; ANON., 1942).

In September 1895, the two shell collections were merged when their owners married and moved into a house on Signal Hill in Long Beach. At the time of their marriage, William H. Dall wrote them:

"Speaking from experience I may compare married folks to the two valves of a clam, different, yet, in a sense, equal; necessary to each other for completeness; liable to nip anybody who comes between them; showing to the outside world what ever of strength and beauty they possess, yet sheltering from observation all that is most precious, tender and necessary to life, between

them. Quiet contentment is proverbial of clams and not to be despised by human beings; they are also said to be happy at high water, which I hope will never fail you. They enclose and foster the 'pearl of great price,' referred to in scripture, and emblematic of all that is lovely in the marriage relation. Let us not forget their example. May care and sorrow follow you at a snail's pace and never catch up with you. May good fortune stick to you like an abalone to a rock, and your friends be as numerous as *Littorinas.*"[2]

With his skills in carpentry, Tom Oldroyd made cabinets for their collection (KEEN, 1983:11), and together they collected extensively in southern California. While they did little dredging themselves, Tom Oldroyd was very successful in encouraging San Pedro fishermen to bring in shells caught in their nets. As a result, the Oldroyds accumulated extensive suites of many rare taxa, such as *Trophon catalinensis,* which no one else had. Ida Oldroyd became an early and active member of the Conchological Club of Southern California, founded in 1902.

In 1914, Ida Oldroyd went to Oakland, California, to pack a portion of the collection of the late Henry Hemphill for its transfer to the California Academy of Sciences (ANON., 1914; background: COAN & ROTH, 1987). Two years later, some alumni of the Geology Department of Stanford University, through the efforts of the paleontolo-

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[1] His name was Tom, not Thomas, as it has been given by some authors. In every paper he published and on his gravestone, it is Tom. In biographical articles after his death, it is said that he was born in "Huddisfield," England. However, we can find no such place name and suspect that this is an error for Huddersfield.

[2] From a copy in the CAS Archives.

gist Ralph Arnold, purchased the remainder of the Hemphill collection. According to KEEN (1983:12–13):

"None of these alumni had any idea how to lay it out or what to do with it, so someone suggested that the department hire Mrs. Oldroyd to come and unpack, and put the material into cabinets. So she started doing it [in 1916], and immediately saw that part of it, at least, needed reidentification, and so she wanted her own collection to use for comparative purposes. Her collection had been sent, a piece at a time, to the U.S. National Museum so she felt that the labels were authentic, and she could compare Hemphill's things with hers and get the proper reidentification. So, the department consented that she could bring her collection up, which she did. She put it out in cabinets on one side of the room and unpacked the Hemphill material on the other side. Then, after she got the Hemphill stuff all out, she called the department in and said, 'Now, look, why don't you just want to buy my collection and have it as [a] supplement, and then you will have the best collection on the coast?' So they talked it over and decided to do that [in 1917]. But they didn't have money enough to buy it outright; the Oldroyds wanted several thousand dollars for it. So the department then offered to hire the Oldroyds on an annual basis, paying them what was . . . called an annuity, but it was actually . . . installments on the collection. So, she was to be curator until the $8,000 amount was paid off. But by the time she got installed, that arrangement was largely forgotten, and she always felt she had an annuity for life, and nobody disputed her, so she stayed on until she was about 84, [when] she died."

While at Stanford, the Oldroyds also kept up their extensive collecting, with dredging expeditions—near Friday Harbor, Puget Sound, during the summers of 1917 (T. OLDROYD, 1918a) and 1918 (I. OLDROYD, 1919), and near Nanaimo, British Columbia, in May 1919 (I. OLDROYD, 1920:135) and in July and August 1934 (I. OLDROYD, 1935a:14; 1935b). In 1922, Ida Oldroyd was hired by the American Museum of Natural History as a consultant in conchology. She spent several months there evaluating and arranging the collection, and she provided many West Coast shells, including some type specimens, by later exchange.

In 1929–1930, the two traveled around the world (Figures 2, 3). On their return, they engaged in extensive overseas exchanges and acquired several entire collections for the university.

Ida Oldroyd was a charter member of the American Malacological Union. At its first meeting in 1931, she gave a paper entitled "Shells that have strayed far from home" (ANON., 1931:2). At the 1933 meeting, she presented "Notes on some of the West Coast Veneridae" (ROBERTSON, 1933: 38). The 1934 AMU meeting was held at Stanford University, and Mrs. Oldroyd gave the welcoming address on

"The history of the Stanford collection" as well as a paper titled "The uses and abuses of shells." She was there elected Honorary President, a post she retained until her death. She evidently attended all of the AMU meetings, except that held in 1932, and she presented papers at most of them (I. OLDROYD, 1935b, 1936, 1938). Oddly, although she is not listed among the attendees at the meeting in Havana in 1938 (AMU *Bulletin* for 1938:[15]), CHACE (1940) told the story of how, having missed the boat to Cuba, she flew there from Florida and arrived before the rest of the AMU members.

Tom Oldroyd died 3 November 1932 (ANON., 1932). His particular contribution was the study of Pleistocene fossils. He was especially interested in minute shells, and his paper on the Pleistocene fossils from the Nob Hill Cut in San Pedro (T. OLDROYD, 1925) has lengthy descriptions of many pyramidellids proposed as new taxa.

Myra Keen, having received her PhD at the University of California in Berkeley in 1934, returned to join her parents in Palo Alto. There being few jobs in her chosen field of psychology, she became a volunteer assistant to Mrs. Oldroyd, with the task of identifying and curating land snails. However, Mrs. Oldroyd had very set ideas about how things should be done, and the two did not get along. After about four months, Keen took the opportunity to become a research assistant to the paleontologist Hubert G. Schenck (KEEN, 1983; ROBERTSON, 1986).

Ida Oldroyd died on 9 July 1940 (ANON., 1942). She was particularly noted for her books on the mollusks of Puget Sound (I. OLDROYD, 1924b) and on those of the entire northeastern Pacific (I. OLDROYD, 1925, 1927). Both works are essentially non-critical compilations of original descriptions, but with many new illustrations.

The Stanford University collections were transferred to the California Academy of Sciences on 9 March 1977 (SMITH, 1978).

LIST OF TAXA
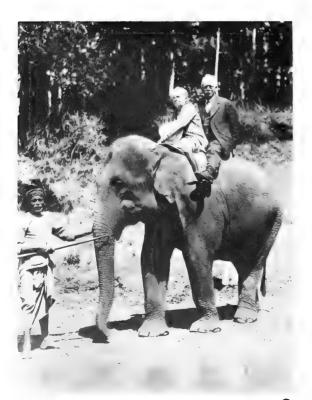
The following list includes the taxa that the Oldroyds introduced. Each original combination is followed by the original reference (keyed to the Literature Cited). This is followed by the type locality (with added data in brackets), information about type material (number of specimens in parentheses), and any remarks about current allocation. The Literature Cited provides references for the Oldroyds' taxa, any senior homonyms of these taxa, and sources of information about their current allocation, but not for senior synonyms of the taxa; references for papers on mollusks not containing new taxa are also included. Three *nomina nuda* are allocated to the synonymy of other species based on material labeled by Ida Oldroyd in the California Academy of Sciences.

The pages numbered in I. OLDROYD (1927) are those of the entire set of three volumes (1–941), rather than the separate page numbers also present in volumes 2 and 3.

The Oldroyds can be assumed to be the collectors unless

otherwise indicated. Prior collection numbers, such as those of the Stanford University Paleontology Type Collection (SMITH, 1978), are not given here. We have relied upon published type catalogues for the holdings of the Los Angeles County Museum of Natural History (SPHON, 1971, 1973; WILSON & BING, 1970; WILSON & KENNEDY, 1967), the San Diego Natural History Museum (WILSON, 1966), and the University of Colorado Museum (WU & BRANDAUER, 1982).

The following abbreviations are used for institutions in the list.

AMNH—American Museum of Natural History, New York

CAS—California Academy of Sciences, San Francisco

LACM—Los Angeles County Museum of Natural History

LACMIP—LACM, Department of Invertebrate Paleontology

SBMNH—Santa Barbara Museum of Natural History

SDNHM—San Diego Natural History Museum

UCM—University of Colorado Museum, Boulder

UCMP—University of California, Museum of Paleontology, Berkeley

UCR—University of California, Riverside

USNM—United States National Museum of Natural History, Washington, D.C.

Cnidaria

oldroydi, Dendrophylla—I. OLDROYD, 1925:pl. 49, fig. 7, *ex* FAUSTINO MS. See also FAUSTINO, 1931:286–287, 289; pl. 1, fig. 2.

[Submarine canyon] off San Pedro, Los Angeles Co., Calif.; 366 m.

Type material: CAS 036397, holotype, 8 pieces of colony; UCMP 12200, "paratype."

Remarks: *Dendrophylla oldroydi* I. Oldroyd, 1925; *D. oldroydi* Faustino, 1931, is an objective synonym and a junior primary homonym. See DURHAM (1947:38, 57; pl. 10, figs. 1, 9).

Annelida

nodosus, Vermetus—T. OLDROYD, 1921a:116, 119; pl. 5, fig. 10.

Nob Hill Cut, San Pedro, Los Angeles Co., Calif.; San Pedro Sand; middle Pleistocene[3].

Type material: CAS 61823.03, holotype.

Remarks: Described as a vermetid gastropod, Keen (*in* SMITH, 1978:352) concluded that it was a burrow lining of a teridinid bivalve. R. D. Turner (letter, 30 May 1989) disagreed, as do we. It seems instead to be the tube of a serpulid worm, perhaps *Protula superba* Moore, 1909 (based on examination of preserved material in the CAS). However, its allocation merits additional investigation.

Mollusca

Bivalvia

austini, Leda—I. OLDROYD, 1935a:13–14; fig. 2.

Off Neck Point, W coast of Vancouver Id., British Columbia; 183 m.

Type material: CAS 060973, holotype, right valve; CAS 060974, paratype. Holotype evidently not deposited at Pacific Biological Station as indicated by I. Oldroyd (F. R. Bernard, letter, 7 April 1987).

Remarks: Synonym of *Nuculana* (*Thestyleda*) *spargana* Dall, 1916, according to BERNARD (1983:13).

clemensae, Pecten—I. OLDROYD, 1938:[2] [*nomen nudum*].

Remarks: Synonym of *Chlamys* (*Chlamys*) *rubida* (Hinds, 1845), based on material labeled by I. Oldroyd in the CAS.

clemensi, Pecten hindsii—I. OLDROYD, 1935b:[3] [*nomen nudum*].

Remarks: Synonym of *Chlamys* (*Chlamys*) *rubida* (Hinds, 1845), based on material labeled by I. Oldroyd in the CAS.

gardneri, Yoldia—I. OLDROYD, 1935a:14; fig. 1.

"Gardner" [Garden] Bay, Pender Harbor, Vancouver Island, British Columbia; 7 m.

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[3] This locality is U.S. Geological Survey location 10419. The terminology for this formation and its age have been brought into conformity with modern usage.

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Explanation of Figures 1 to 4

Figure 1. Tom and Ida Oldroyd, about 1900.

Figure 2. Ida and Tom Oldroyd aboard the *Empress of Australia,* 1929.

Figure 3. Ida and Tom Oldroyd, Elephant Park, Colombo, Sri Lanka, 1930.

Figure 4. Tom and Ida Oldroyd at a beach shanty in Long Beach, California, about 1900. The person in the middle is unidentified.

Type material: CAS 060975, holotype, pair; CAS 060976 (1), 064888 (2), paratypes. Holotype evidently not deposited at Pacific Biological Station as indicated by I. Oldroyd (F. R. Bernard, letter, 7 April 1987).

Remarks: Synonym of *Yoldia (Yoldia) amygdalea* (Valenciennes, 1846), according to BERNARD (1983:13).

kincaidi, Pecten—I. OLDROYD, 1920:135–136; pl. 4, figs. 3, 4. See also I. OLDROYD, 1924b:17; pl. 9, figs. 3, 4; 1925:53–54; pl. 12, figs. 1, 2, both as *Pecten hindsii kincaidi.*

[Puget Sound, Washington; 46 m (label)]; July 1919 (holotype); July 1918 (paratype).

Type material: CAS 064277, holotype; the paratype cannot be located in the Thomas Burke Memorial Washington State Museum at the University of Washington (E. Marshall, letter, 30 September 1989).

Remarks: Synonym of *Chlamys (Chlamys) rubida* (Hinds, 1845), according to BERNARD (1983:25).

lomitensis, Crassatellites—I. OLDROYD, 1924a:10; pl. C.

Lomita, Los Angeles Co., Calif.; Lomita Marl; middle Pleistocene; S. M. Purple.

Type material: UCR 6621/1, holotype, a left valve. Not deposited in LACMIP, as indicated. Oldroyd implied that the type specimen included both valves but illustrated only the left valve, and a right valve was not located by MOUNT (1974).

Remarks: Synonym of *Eucrassatella fluctuata* (Carpenter, 1864), according to COAN (1984:158).

meridonalis, Chione—I. OLDROYD, 1921:93; pl. 4, figs. 3, 4.

[Sechura Bay (label)] Peru.

Type material: UCMP 31206, UCMP Loc. 3135, holotype, pair; CAS 064399, paratype.

Remarks: Synonym of *Chione (Chione) compta* (Broderip, 1835), according to BERNARD (1983:51).

nana, Cuspidaria (Tropidomya)—I. OLDROYD, 1918b: 28. See also I. OLDROYD, 1925:99; pl. 13, figs. 8, 9.

Monterey Bay, Monterey Co., Calif.; clay; 2 specimens. Also, Bolinas, Marin Co., Calif.; H. Hemphill; 1 specimen.

Type material: CAS 060981, holotype, pair, from Monterey Bay; AMNH 58306, paratype, pair, from Monterey Bay.

Remarks: Synonym of *Sphenia luticola* (Valenciennes, 1846), according to BERNARD (1983:58).

newcombi, Pecten—I. OLDROYD, 1938:[2] [*nomen nudum*].

Remarks: Synonym of *Chlamys (Chlamys) hastata* (Sowerby, 1843), based on material labeled by I. Oldroyd in the CAS.

pugetensis, Pecten islandica—I. OLDROYD, 1920:136; pl. 4, figs. 5, 6. See also I. OLDROYD, 1924b:18, 209; pl. 9, figs. 5, 6; 1925:55; pl. 12, figs. 4, 5.

San Juan Islands, San Juan Co., Puget Sound, Washington; 12 specimens (2 dredged, 10 on shore); [1920 (label in SBMNH)].

Type material: CAS 064278, holotype, pair; CAS 066375, paratypes (6), from rocks on shore opposite Turn Id. (label); SBMNH 34893, paratype, pair; AMNH 30549, paratype, pair.

Remarks: Synonym of *Chlamys (Chlamys) hastata* (Sowerby, 1843), according to BERNARD (1983:24).

Gastropoda

amava, Odostomia (Ivara)—T. OLDROYD, 1925:14, 29, 38; pl. 1, fig. 7.

Nob Hill Cut, San Pedro, Los Angeles Co., Calif.; San Pedro Sand; middle Pleistocene; 1 specimen.

Type material: USNM 352514, holotype.

angelena, Olivella biplicata—T. OLDROYD, 1918b:34–35. See also T. OLDROYD, 1921:119; pl. 5, fig. 6; I. OLDROYD, 1927:161; pl. 26, figs. 17, 17a, both as *O. b.* "angelina."

San Pedro, Los Angeles Co., Calif.; living as well as in "upper" [Palos Verdes Sand; late Pleistocene] and "lower" [San Pedro Sand; middle Pleistocene] San Pedro Formation.

Type material: CAS 064312, holotype; CAS 064313 (1), 065621 (12), SBMNH 34839 (1), paratypes, from the Recent fauna. CAS 66181.01 (13), paratypes, from the upper Pleistocene at Santa Monica, Los Angeles Co., Calif. CAS 66182.01 (22), paratypes, from the upper Pleistocene at Signal Hill, Long Beach, Los Angeles Co., Calif.

Remarks: Synonym of *Olivella biplicata* (Sowerby, 1825), according to BURCH & BURCH (1959:20).

angelica, Acanthina—I. OLDROYD, 1918a:26–27.

Bahía Redondo, Isla Angel de la Guarda, Baja Calif. [Norte]; L. C. Decius & A. D. Fyfe, November 1917.

Type material: CAS 064396, holotype.

Remarks: *Acanthina angelica* I. Oldroyd, according to KEEN (1971:551, 552; fig. 1082), who illustrated the holotype and what was said to be a paratype. The latter has not been located.

buttoni, Cypraea undata—I. OLDROYD, 1916:107–108.

Fiji Islands; [collector unknown].

Type material: CAS 064143, holotype; AMNH 44439, paratype.

Remarks: Unnecessarily renamed *Palmadusta diluculum virginalis* SCHILDER & SCHILDER (1938:160). Synonym of *Cypraea diluculum* Reeve, 1845, according to BURGESS (1985:129).

californicum, Sinum—I. OLDROYD, 1917:13. See also I. OLDROYD, 1927:732–733; pl. 92, figs. 13, 14.

San Pedro, Los Angeles Co., Calif.; 10 specimens.

Type material: CAS 064357, holotype; CAS 067160 (1), 067161 (5), paratypes.

Remarks: Synonym of *Sinum scopulosum* (Conrad, 1849), according to MARINCOVICH (1977:350).

catalinensis, Trophon—I. OLDROYD, 1927:327; pl. 34, figs. 1, 2.

Off San Pedro, Los Angeles Co., Calif.; 46 m.

Type material: CAS 063306, holotype; CAS 036367 (7), 063307 (1), 063308 (1), 063309 (1), 065618 (17), SBMNH 34837 (2), paratypes; CAS 065617 (2), 065619 (1), 065620 (3), probable paratypes.

Remarks: *Trophon (Austrotrophon) cerrosensis catalinensis* I. Oldroyd, according to ABBOTT (1974:191). The Oldroyds distributed many lots of this species at the turn of the century under other names, long before it was named by I. Oldroyd; these specimens are not regarded as being types.

civitella, Odostomia (Evalea)—T. OLDROYD, 1925:15, 32–33, 38; pl. 1, fig. 7.

Nob Hill Cut, San Pedro, Los Angeles Co., Calif.; San Pedro Sand; middle Pleistocene; 16 specimens.

Type material: USNM 352523, holotype; USNM 352524 (5), CAS 61823.04 (4), paratypes.

clarki, Epitonium—T. OLDROYD, 1921a:115, 119; pl. 5, fig. 13.

[Potrero Canyon], Santa Monica [Los Angeles], Los Angeles Co., Calif.; late Pleistocene; F. C. Clark[4].

Type material: CAS 66041.02, holotype; CAS 66041.01 (2), 66042.01 (2), paratypes.

Remarks: Synonym of *Asperiscala minuticosta* (DeBoury, 1912), according to DuSHANE (1979:103).

collisella, Turbonilla (Pyrgolampros)—T. OLDROYD, 1925:14 [as "*collisellae*"; first revision herein]; 25–26, 38; pl. 1, fig. 11.

Nob Hill Cut, San Pedro, Los Angeles Co., Calif.; San Pedro Sand; middle Pleistocene; 29 specimens.

Type material: USNM 333507, holotype; USNM 352507 (1), CAS 61823.05 (10), LACMIP 2157-2158 (2), paratypes.

continuatum, Epitonium—T. OLDROYD, 1925:13, 35, 39; pl. 2, fig. 10.

Nob Hill Cut, San Pedro, Los Angeles Co., Calif.; San Pedro Sand; middle Pleistocene; "2 specimens" (p. 13), "1 specimen" (p. 35), the latter probably correct.

Type material: USNM 352383, holotype.

Remarks: Synonym of *Nitidiscala tincta* (Carpenter, 1865), according to DuSHANE (1979:117).

diegensis, Clathrodrillia—T. OLDROYD, 1921a:115–116, 119; pl. 5, fig. 12.

Pacific Beach, San Diego Co., Calif.; "upper Pleistocene" [?San Diego Formation; late Pliocene]; H. Hemphill; 4 specimens.

Type material: UCMP 31207, holotype; CAS 66042.01 (3), paratypes.

Remarks: Synonym of *Moniliopsis graciosana mercedensis* (Martin, 1914), according to GRANT & GALE (1931:569). Genus originally misspelled "*Clathrodrilla.*"

diegensis, Olivella boetica—T. OLDROYD, 1921b:118, 119; pl. 5, fig. 2. See also I. OLDROYD, 1927:163; pl. 26, figs. 18, 18a.

[San Diego, San Diego Co., Calif. (labels)]. Also upper San Pedro [Palos Verdes Sand]; late Pleistocene.

Type material: CAS 064353, holotype; CAS 067156 (23), 067157 (77), SBMNH 34841 (1), paratypes, from the Recent fauna. CAS 66181.01 (many), paratypes, from the upper Pleistocene at Santa Monica, Los Angeles Co.; CAS 66183.01 (100), paratypes, from the upper Pleistocene at San Pedro, Los Angeles Co., Calif.

Remarks: Synonym of *Olivella baetica* Carpenter, 1864, according to BURCH & BURCH (1959:9).

epiphanea, Turbonilla (Mormula)—T. OLDROYD, 1925:14 [as "*epiphania*"; first revision herein]; 28–29, 38; pl. 1, fig. 12.

Nob Hill Cut, San Pedro, Los Angeles Co., Calif.; San Pedro Sand; middle Pleistocene; 30 specimens.

Type material: USNM 333510, holotype?; USNM 352510 (5), CAS 61823.06 (3), LACMIP 2169 (1), paratypes.

fitella, Odostomia (Evalea)—T. OLDROYD, 1925:15, 33, 38; pl. 1, fig. 8.

Nob Hill Cut, San Pedro, Los Angeles Co., Calif.; San Pedro Sand; middle Pleistocene.

Type material: USNM 352525, holotype; USNM 352526 (2), CAS 61823.07 (2), paratypes.

fossilis, Conus californicus—T. OLDROYD, 1921a:116, 119; pl. 5, fig. 9.

Nob Hill Cut, San Pedro, Los Angeles Co., Calif.; San Pedro Sand; middle Pleistocene: "not rare" (T. OLDROYD, 1925:10). Also in "upper San Pedro beds" [Palos Verdes Sand; late Pleistocene].

Type material: CAS 61823.08, holotype; CAS 61823.23 (3), 61823.24 (6), USNM 35352 (5), SDNHM 361-362 (2), paratypes, from Nob Hill Cut. CAS 66182.04 (5), paratypes, from the upper Pleistocene at Signal Hill, Long Beach, Los Angeles Co., Calif.

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[4] For information on this locality, see VALENTINE (1956).

Remarks: Synonym of *Conus californicus* Hinds, 1844, according to GRANT & GALE (1931:472–473).

fraseri, Tritonalia—I. OLDROYD, 1920:135; pl. 4, figs. 1, 2. See also I. OLDROYD, 1924b:101, 209; pl. 9, figs. 1, 2; 1927:323–324; pl. 30, figs. 11, 11a.

Brandon Island, Departure Bay, Vancouver Island, British Columbia; May 1919.

Type material: CAS 064275, holotype; CAS 064276 (2), 064837 (14), 066374 (7), USNM 338431 (5), SBMNH 34836 (1), SDNHM 1636 (1), UCM 21492 (5), paratypes.

Remarks: Synonym of *Ocenebra interfossa* (Carpenter, 1864), according to RADWIN & D'ATTILIO (1976:122–123).

fucana, Olivella biplicata—T. OLDROYD, 1921b:118, 119; pl. 5, fig. 4. See also I. OLDROYD, 1924b:88, 213; pl. 22, fig. 2; 1927:161; pl. 26, figs. 23, 23a.

Near Cape Flattery, Straits of Juan de Fuca, Washington. Also "Pliocene at San Pedro" [Timms Point Silt; middle Pleistocene].

Type material: CAS 064355, holotype; CAS 067153, paratypes (3), all from the Recent fauna.

Remarks: Synonym of *Olivella biplicata* (Sowerby, 1825), according to BURCH & BURCH (1959:19–20).

gomphina, Odostomia (Chrysallida)—T. OLDROYD, 1925: 14, 29–30, 38; pl. 1, fig. 3.

Nob Hill Cut, San Pedro, Los Angeles Co., Calif.; San Pedro Sand; middle Pleistocene; 2 specimens.

Type material: USNM 352515, holotype; CAS 61823.09, paratype.

hemphilli, Tegula—T. OLDROYD, 1921a:115, 119; pl. 5, figs. 11, 11a.

"Upper Pleistocene" [?Pliocene; San Diego Formation (G. L. Kennedy, verbal communication, 25 October 1989)]; Pacific Beach, San Diego Co., Calif.; H. Hemphill; 5 specimens.

Type material: UCMP 31208, holotype; UCMP 14975 (1), CAS 66042.02 (3), paratypes.

Remarks: A valid, extinct Pliocene and Pleistocene species of *Tegula* (*Agathistoma*), according to KENNEDY (1973:123–124; figs. 3a,b) and J. H. McLean (letter, 3 May 1989).

himerta, Turbonilla (Pyrgiscus)—T. OLDROYD, 1925: 14, 27–28, 38; pl. 1, fig. 1.

Nob Hill Cut, San Pedro, Los Angeles Co., Calif.; San Pedro Sand; middle Pleistocene; 5 specimens.

Type material: USNM 333508, holotype; USNM 352509 (1), CAS 61823.10 (2), paratypes.

hybrida, Acmaea pelta var.—I. SHEPARD [OLDROYD], 1895:72 [*nomen nudum*].

Remarks: BURCH (1946:11) quoted a description of this variety, supposedly from OLDROYD's (1895) paper, but no description is present there. Where this quotation came from is a mystery; perhaps he was quoting the contents of a letter and misunderstood the writer's description to be that of Oldroyd. In any event, the taxon seems to have first been made available by Burch, but potential type material cannot now be found in the portion of the Burch collection in the possession of Tom and Beatrice Burch (B. L. Burch, letter, 26 July 1989). KEEP (1910:331) credited this name to Hemphill, but it is a *nomen nudum* everywhere it has appeared other than in BURCH (1946). Burch's taxon is a synonym of *Lottia pelta* (Rathke, 1833).

idae, Turbonilla (Pyrgolampros)—T. OLDROYD, 1925: 14, 26–27, 38; pl. 1, fig. 9.

Nob Hill Cut, San Pedro, Los Angeles Co., Calif.; San Pedro Sand; middle Pleistocene; 190 specimens.

Type material: USNM 333509, holotype; USNM 352508 (38), 352533 (1), CAS 61823.01 (20), 61823.02 (101), 61823.26 (many), LACMIP 2159-2168 (10), paratypes. The contents of USNM 352508 and 352533 are opposite in terms of number of specimens from those given in T. Oldroyd's paper.

indisputabilis, Alectrion cooperi var.—T. OLDROYD, 1925: 12 [*nomen nudum*; credited to "I.S. Oldroyd, 1921"].

indisputabilis, Alectrion mendicus—I. OLDROYD, 1927: pl. 26, fig. 4 [not in text].

[San Diego, San Diego Co., Calif.; H. Hemphill (label)].

Type material: CAS 064356, holotype.

Remarks: Synonym of *Nassarius mendicus* (Gould, 1851), according to GRANT & GALE (1931:674).

ithea, Odostomia (Evalea)—T. OLDROYD, 1925:14, 31–32, 38; pl. 1, fig. 2.

Nob Hill Cut, San Pedro, Los Angeles Co., Calif.; San Pedro Sand; middle Pleistocene; 2 specimens.

Type material: USNM 352520, holotype; CAS 61823.11, paratype.

magna, Lirularia—T. OLDROYD, 1925:20 [as *Margarites (Lirularia) magna*]; 36, 38; pl. 3, figs. 2, 3, 5.

Nob Hill Cut, San Pedro, Los Angeles Co., Calif.; San Pedro Sand; middle Pleistocene; "most plentiful."

Type material: USNM 352534, holotype (and 1 paratype evidently added later); USNM 352410 (many), CAS 1198.02 (many), 61823.12 (64), 61823.27 (many), 61823.28 (45), 61823.29 (many), LACMIP 2460–2468 (9), SBMNH 34843 (163), paratypes.

Remarks: Synonym of *Lirularia optabilis* (Carpenter, 1864), an extinct Pleistocene species, according to J. H. McLean (verbal communication, 18 February 1989). The number of specimens in the USNM lots differs from those stated in the original publication.

major, Alia tuberosa—T. OLDROYD, 1925:12 [as *Columbella* (*Alia*) *tuberosa major*]; 24, 39; pl. 2, fig. 11.

Nob Hill Cut, San Pedro, Los Angeles Co., Calif.; San Pedro Sand; middle Pleistocene; "plentiful."

Type material: USNM 352369, 13 specimens in one vial and 50 in another, including one isolated that is possibly the holotype (the rest are paratypes); CAS 1198.04 (1), 61823.30 (122), 61823.31 (many), 61823.32 (44), SBMNH 34842 (5), paratypes.

Remarks: Synonym of *Mitrella tuberosa* (Carpenter, 1864), according to GRANT & GALE (1931:697).

manca, Odostomia (*Evalea*)—T. OLDROYD, 1925:15, 32, 38; pl. 1, fig. 5.

Nob Hill Cut, San Pedro, Los Angeles Co., Calif.; San Pedro Sand; middle Pleistocene; 60 specimens.

Type material: USNM 352521, holotype; USNM 352522 (10), CAS 61823.13 (15), LACMIP 2170–2172 (3), paratypes.

menzola, Odostomia (*Amaura*)—T. OLDROYD, 1925:15, 33–34, 39; pl. 2, fig. 6.

Nob Hill Cut, San Pedro, Los Angeles Co., Calif.; San Pedro Sand; middle Pleistocene; 16 specimens.

Type material: USNM 352527, holotype; USNM 352528 (5), CAS 61823.14 (4), LACMIP 2173 (1), paratypes.

mexicana, Olivella boetica—T. OLDROYD, 1921b:118, 119; pl. 5, fig. 3. See also I. OLDROYD, 1927:163; pl. 26, figs. 21, 21a.

Laguna Scammon, Baja Calif. Sur; H. Hemphill. Also living at San Pedro and "upper San Pedro" [Palos Verdes Sand; late Pleistocene].

Type material: CAS 064354, holotype, from Laguna Scammon. CAS 66181.03 (15), paratypes, from upper Pleistocene at Santa Monica, Los Angeles Co., Calif. CAS 66182.02 (43), paratypes from upper Pleistocene at Signal Hill, Long Beach, Los Angeles Co., Calif. CAS 66183.02 (160), paratypes, from Upper Pleistocene at San Pedro, Los Angeles Co., Calif.

Remarks: Synonym of *Olivella baetica* (Carpenter, 1864), according to BURCH & BURCH (1959:9).

minuta, Anachis—T. OLDROYD, 1921a:114–115 [*non Columbella* (*Anachis*) *minuta* GOULD, 1860:334].

[Potrero Canyon], Santa Monica [Los Angeles], Los Angeles Co., Calif.; late Pleistocene; F. C. Clark[4].

Type material: Missing.

Remarks: Possibly a synonym of *Steironepion tincta* (Carpenter, 1864). GRANT & GALE (1931:686–687, 940; pl. 26, figs. 31, 34) made it a synonym of *Pleurotoma lineolata* Reeve, 1846, and KEEN (1971:595–597; fig. 1252) made "*P. lineolata* Reeve," *auctt.*, a synonym of Carpenter's species.

mitchelli, Acmaea striata—I. OLDROYD, 1933:205, 207; pl. 1, figs. 1–4.

Southern Luzon, Philippine Islands; S. A. Mitchell.

Type material: Holotype formerly in Philippine Bureau of Science 16369, but lost during World War II (J. J. Cabrera, letter, 6 June 1989); CAS 064128 (13), paratypes.

Remarks: Synonym of *Patelloida striata* Quoy & Gaimard, 1834, according to D. R. Lindberg (verbal communication, 8 February 1989).

mitchelli, Nerita—I. OLDROYD, 1933:205–207; pl. 1, figs. 5–7.

Philippine Islands; S. A. Mitchell.

Type material: Holotype formerly in Philippine Bureau of Science 16368, but lost during World War II (J. J. Cabrera, letter, 6 June 1989); CAS 064127 (8), 067158 (18), SDNHM 1637–1639 (3), paratypes.

Remarks: Synonym of *Nerita helicinoides* Reeve, 1855.

montereyensis, Astraea inaequalis—I. OLDROYD, 1927: 767–768; pl. 108, figs. 5, 6.

Monterey Bay, Calif.

Type material: CAS 063310, holotype; CAS 066066 (1), 067159 (3), SBMNH 34838 (1), paratypes.

Remarks: Synonym of *Astraea gibberosa* (Dillwyn, 1817), according to SMITH & GORDON (1948:200), although they used the unavailable name *A. inaequalis* (Martyn).

nanella, Marginella jewettii—T. OLDROYD, 1925:11, 24, 39; pl. 2, fig. 8.

Nob Hill Cut, San Pedro, Los Angeles Co., Calif.; San Pedro Sand; middle Pleistocene; "plentiful."

Type material: USNM 352361, lectotype (COAN & ROTH, 1966:291), plus 208 paralectotypes, including one in a gelatin capsule that may have been Oldroyd's holotype; USNM 655952 (15), CAS 1198.03 (33), 61823.15 (169), LACMIP 2152–2154 (3), paralectotypes.

Remarks: Synonym of *Cystiscus jewettii* (Carpenter, 1864) according to COAN & ROTH (1966:291). At the time these authors prepared their study, they were sent a lot of 16 specimens that had been in the USNM Recent collection, and it was deemed necessary to select a lectotype from among them. Unknown to Coan and Roth, however, most of the original lot, including an isolated but unlabeled specimen that may have been set aside as the holotype, was in the USNM fossil collections. Oldroyd's figure and the uniform appearance of this species would make recognition of a holotype virtually impossible.

[*nodosus, Vermetus*—see under Annelida]

oldroydi, Coralliophila—I. OLDROYD, 1929:98–99; pl. 5, figs. 1–4.

Bird Rock, off isthmus, Catalina Id., Los Angeles Co., Calif.; about 1895. Also one specimen from the Galápagos Islands.

Type material: CAS 061746, holotype; CAS 066106 (2), 061747 (1), paratype from Catalina Island; CAS 061748 (1), paratype from the Galápagos.

Remarks: *Latiaxis* (*Babelomurex*) *oldroydi* (I. Oldroyd), according to KEEN (1971:546); see also MCLEAN (1978:45, fig. 23.4). Mrs. Oldroyd named this species after her husband. The Galápagos paratype is probably *L.* (*B.*) *hindsii* Carpenter, 1857 (see KEEN, 1971:545–547; fig. 1068).

parva, Olivella biplicata—T. OLDROYD, 1921b:119; pl. 5, fig. 7. See also I. OLDROYD, 1927:162; pl. 26, figs. 16, 16a.

Punta Abreojos, Baja Calif. Sur; H. Hemphill. Also "upper Pleistocene at San Pedro" [Palos Verdes Sand; late Pleistocene].

Type material: CAS 064314, holotype; CAS 067154 (27), SBMNH 34840 (4), paratypes, from the Recent fauna. CAS 66181.02 (8), paratypes, from the upper Pleistocene at Santa Monica, Los Angeles Co., Calif. CAS 66182.03 (3), paratypes, from the upper Pleistocene at Signal Hill, Long Beach, Los Angeles Co., Calif.

Remarks: Synonym of *Olivella biplicata* (Sowerby, 1825), according to BURCH & BURCH (1959:19–20).

pecora, Turbonilla (*Strioturbonilla*)—T. OLDROYD, 1925: 13, 24–25, 38; pl. 1, fig. 6.

Nob Hill Cut, San Pedro, Los Angeles Co., Calif.; San Pedro Sand; middle Pleistocene; 5 specimens.

Type material: USNM 333506, holotype; USNM 352503 (1), CAS 61823.16 (6), LACMIP 2155–2156 (2), paratypes. Additional material seems to have been added to the type series at a later date.

pedroensis, Acteocina—T. OLDROYD, 1925:9, 23–24, 39; pl. 2, fig. 9.

Nob Hill Cut, San Pedro, Los Angeles Co., Calif.; San Pedro Sand; middle Pleistocene; "plentiful."

Type material: USNM 352346, holotype (missing), plus 5 paratypes; CAS 61823.17 (3), CAS 61823.25 (25), paratypes. None of the USNM paratypes matches the measurements of the holotype given by T. Oldroyd.

Remarks: Synonym of *Acteocina culcitella* (Gould, 1853), according to T. M. Gosliner (verbal communication, 24 May 1989).

sanesia, Odostomia (*Amaura*)—T. OLDROYD, 1925:15, 34–35, 38; pl. 1, fig. 4.

Nob Hill Cut, San Pedro, Los Angeles Co., Calif.; San Pedro Sand; middle Pleistocene; 2 specimens.

Type material: USNM 352531, holotype; CAS 61823.18, paratype.

scelera, Odostomia (*Chrysallida*)—T. OLDROYD, 1925: 14, 30–31, 38; pl. 1, fig. 4.

Nob Hill Cut, San Pedro, Los Angeles Co., Calif.; San Pedro Sand; middle Pleistocene; 9 specimens.

Type material: USNM 352516, holotype; USNM 352517 (2), CAS 61823.19 (3), paratypes.

taylori, Tegula pulligo—I. OLDROYD, 1924b:171–172, 211; pl. 20, figs. 1, 2. See also I. OLDROYD, 1927:781–782; pl. 91, figs. 3, 6 (listed in both accounts as "1922," but there is no such publication).

Hope Island, N end Vancouver Id., British Columbia; G. W. Taylor.

Type material: CAS 060977, holotype; CAS 060978 (1), 066746 (1), paratypes.

Remarks: Synonym of *Tegula pulligo* (Gmelin, 1791), according to SMITH & GORDON (1948:201).

tersa, Odostomia (*Evalea*)—T. OLDROYD, 1925:14, 31, 38; pl. 1, fig. 10.

Nob Hill Cut, San Pedro, Los Angeles Co., Calif.; San Pedro Sand; middle Pleistocene; 6 specimens.

Type material: USNM 352518, holotype; USNM 352519 (2), CAS 61823.20 (2), paratypes.

timessa, Odostomia (*Amarua*)—T. OLDROYD, 1925:15, 35, 39; pl. 2, fig. 4.

Nob Hill Cut, San Pedro, Los Angeles Co., Calif.; San Pedro Sand; middle Pleistocene; 3 specimens.

Type material: USNM 352532, holotype; USNM 353400 (2), CAS 61823.21 (15), LACMIP 2174–2175 (2), paratypes. Because the total number of type specimens is far in excess of the three originally specified, additional material seems to have been added to the type series at a later date.

trochilia, Odostomia (*Amaura*)—T. OLDROYD, 1925:15 [as *O.* "*trochila*"; first revision herein]; 34, 39; pl. 2, fig. 1.

Nob Hill Cut, San Pedro, Los Angeles Co., Calif.; San Pedro Sand; middle Pleistocene; 2 specimens.

Type material: USNM 352529, holotype; USNM 352530 (1), paratype.

tumida, Tornatina—T. OLDROYD, 1921a:116, 119; pl. 5, fig. 8. See also T. OLDROYD, 1925:9, as *Acteocina tumida*.

Nob Hill Cut, San Pedro, Los Angeles Co., Calif.; San Pedro Sand; middle Pleistocene.

Type material: USNM 353399, holotype.

Remarks: This seems to be a *Retusa*, according to T. M. Gosliner (verbal communication, 24 May 1989).

vancouverensis, Acteon punctocoelata—I. OLDROYD, 1927: 25; pl. 1, figs. 19, 20.

[Brandon Island], Departure Bay, Vancouver Id., British Columbia; 5 m.

Type material: CAS 060979 (1), 060980 (1), syntypes; LACM 1078 (1), "paratype."

Remarks: Synonym of *Acteon punctocaelatus* (Carpenter, 1864), according to GRANT & CALE (1931:443).

ACKNOWLEDGMENTS

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Calcium Source for Protoconch Formation in the Florida Apple Snail, *Pomacea paludosa* (Prosobranchia: Pilidae): More Evidence for Physiologic Plasticity in the Evolution of Terrestrial Eggs

by

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Abstract. The calcified capsule of terrestrial eggs of several gastropods is known to provide calcium as well as structural support for the embryo. This study examined capsular ultrastructure and intracapsular calcium content of the terrestrial eggs of the aquatic Florida apple snail, *Pomacea paludosa*. The calcium content of intracapsular material did not increase during embryogenesis of *P. paludosa*, and little erosion of the capsule was evident by scanning electron microscopy. Initial intracapsular calcium concentration was 745 mM, far higher than values reported for other gastropods. These results indicate that the embryo of *P. paludosa* is independent of capsular calcium. Reliance of the embryo on intracapsular, rather than capsular, stores of calcium for protoconch formation is a strategy not recognized before among gastropods but is one that has a parallel among squamate reptiles.

INTRODUCTION

Many families of gastropods have independently evolved calcified terrestrial eggs. The more heavily calcified eggs are cleidoic, and those of a few species have been directly or indirectly shown to resorb calcium from the eggshell (TOMPA, 1980). Uncalcified eggs are non-cleidoic and absorb calcium from the extracapsular environment. TOMPA (1980) described the diversity of embryonic calcium dynamics in gastropods. He proposed that calcified egg capsules evolved in terrestrial gastropods to provide not only structural support to the capsule but also calcium for embryonic shell (protoconch) formation. Furthermore, he hypothesized that, despite the diversity of adaptations for embryonic calcium provision in gastropods, intracapsular concentrations of calcium must remain low in the newly oviposited egg to prevent toxicity. In the present study, we report the changes in intracapsular calcium content during embryogenesis of the Florida apple snail, *Pomacea paludosa* (Say, 1829). Unlike other species previously studied, the terrestrial embryos of this aquatic, prosobranch snail do not depend on the capsule for calcium; this is a strategy of calcium provision that extends the known range of physiologic plasticity in gastropod eggs.

MATERIALS AND METHODS

Egg clutches of *Pomacea paludosa* were collected from emergent vegetation at ponds in West Melbourne, Florida. Voucher specimens of adult snails (IRCZM 065:02878) and of clutches and an adult shell (IRCZM 065:02879) are deposited at the Indian River Coastal Zone Museum, Harbor Branch Oceanographic Institution, Fort Pierce, Florida.

Freshly laid (jellied) clutches were collected in early morning and processed upon return to the laboratory. Individual eggs were teased from the extracapsular jelly and transferred to a dish of distilled water. The capsule was slit, spread open, and evacuated of contents (egg fluids,

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Table 1

Changes in dry weight and calcium content of *Pomacea paludosa* during intracapsular development. Each sample consists of pooled intracapsular contents of 10 newly oviposited eggs or of pooled shells or pooled bodies from 10 hatchlings. "Shell" of hatchlings consists of the protoconchs and opercula; "body" includes all soft parts. Values are $\bar{x} \pm$ SD.

Sample (n = 4)	Dry weight (mg/egg)	Calcium content	
		(mg/egg)	(% dry weight)
Egg	5.64 ± 1.166	1.03 ± 0.286	18.3
Hatchling			
Shell	2.90 ± 0.037	0.933 ± 0.0229	32.2
Body	1.78 ± 0.113	0.033 ± 0.0038	1.8
Total	4.68 ± 0.109	0.967 ± 0.0224	20.7

sensu FOURNIÉ & CHÉTAIL [1984]; including zygote, perivitelline albumen, perivitelline sac, and intracapsular jelly [BAYNE, 1966]) by pipette. When properly removed, the albumen and zygote were invested by a membrane; a sample was discarded if the membrane ruptured during evacuation. For each of four clutches, the contents of 10 eggs were pooled for analysis.

Old clutches with well-calcified capsules and the opaque white color of late-stage eggs (PERRY, 1973) were collected from the field and held in the laboratory in dry beakers until hatching. Adherent pieces of calcified capsule were removed from the protoconch (body shell at hatching) and mantle cavity. Hatchlings were dissected to separate the soft parts from the protoconchs and opercula. Because moderate desiccation greatly decreased the tendency of the soft parts to separate cleanly from the protoconchs and opercula, snails were dissected within 2 hr after hatching. Body parts of 10 hatchlings were pooled for each of four sets of samples, each set consisting of a pooled sample of soft parts and a pooled sample of protoconchs and opercula.

Samples were dried to constant weight at 68°C in acid-cleaned beakers and digested in 1 mL 6 N HCl for 2 hr at 68°C. Cooled samples were brought to 10 mL with 6 N HCl , diluted serially with 0.4% La_2O_3 to reduce ionization interference, and analyzed for calcium with a Perkin-Elmer model 4000 atomic absorption spectrophotom-

eter with background correction. Values were corrected also by analysis of blanks that were similarly processed.

Capsular material for scanning electron microscopy was prepared from freshly laid eggs and from eggs hatched in the laboratory. Pieces of capsule were treated with 5.25% NaOCl to remove remnants of the intracapsular contents, air-dried, mounted on aluminum stubs, sputter-coated with gold-palladium alloy, and examined with a Zeiss Novascan 30 scanning electron microscope for physical evidence of calcium resorption from the inner capsular layer.
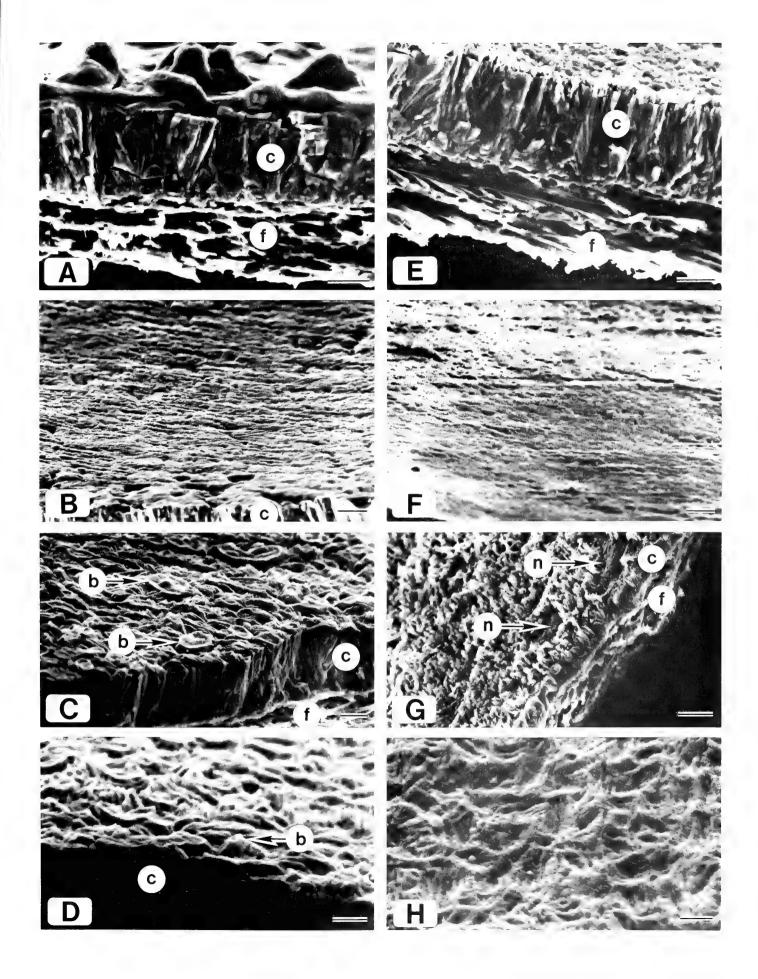
RESULTS

The mean dry weight of intracapsular fluids of the newly oviposited egg was 5.6 mg, of which 1.0 mg (18%) was calcium (Table 1). Assuming a spherical egg with a diameter of 4.0 mm, the intracapsular concentration of calcium was 745 mM. During approximately 3 weeks of development from oviposition to hatching, dry weight of the intracapsular contents decreased 17% (Table 1). Because the weights of contents of the freshly laid eggs were highly variable among clutches, the loss in weight was not statistically significant ($t = 1.640$, df = 3, $P > 0.05$). Calcium content of the intracapsular material decreased slightly (6%); but this, too, was not statistically significant ($t = 0.460$, df = 3, $P > 0.05$). The amount of calcium expressed as percent dry weight of the egg fluids or the hatchling was similar (18% and 21%, respectively). At hatching, most of the calcium (97%) was in the protoconch and operculum.

The inner, crystalline layer of the thick, calcified capsule changed little in physical appearance during embryogenesis; but its structural integrity seemed to be modified, perhaps by degradation of the organic matrix and mineral recrystallization, making it susceptible to disaggregation by NaOCl (Figure 1). Although thickness of the crystalline layer varied among eggs, the layer did not thin noticeably by the time of hatching, nor did the fracture surface change appearance (Figure 1A, E). Brief (<1-min) treatment with NaOCl only partly removed the organic membrane lining the inside of the capsule (Figure 1B, F). In newly oviposited eggs, longer (20-min) treatment with NaOCl completely removed the membrane, exposing the proximal free surfaces of the capsular crystals (Figure 1C); integrity of the balanoid facets of the crystals was maintained when

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Figure 1

Appearance of the fracture and inner surfaces of the egg capsule of *Pomacea paludosa* at oviposition (A–D) and hatching (E–H). A, E: fracture surface of inner, crystalline layer (c) and middle, fibrous layer (f) of the capsule. B, F: oblique views of inner surface of capsule near a fracture surface, treated <1 min with NaOCl; much of inner organic membrane remains. C, G: oblique views of inner surface after 20-min treatment with NaOCl; n, naked patches of deeper crystalline layer exposed by loss of fine, surficial crystals; b, representative balanoid facets. D, H: oblique views of inner surface after 40-min treatment with NaOCl. Scale bars: A, C–E, G–H, 10 μm; B, F, 20 μm.

treatment was extended to 40 min (Figure 1D). In hatched eggs, 20-min treatment with NaOCl exposed a layer of fine, vertically oriented crystals, patches of which broke free and revealed a deeper, more stable surface (Figure 1G); 40-min treatment removed all fine crystals, and the deeper layer appeared to have a negative image of the balanoid facets (Figure 1H).

DISCUSSION

Calcium dynamics in somatic and reproductive physiology have been studied in snails nominally assigned to *Pomacea paludosa* (MEENAKSHI *et al.*, 1974, 1975; WATABE *et al.*, 1976; MEENAKSHI & WATABE, 1977). The snails differ, however, from *P. paludosa* in egg size, capsular ultrastructure, clutch size and morphology, hatching time, and protoconch size (PERRY, 1973; McCabe & Turner, unpublished data). Moreover, they differ in calcium dynamics during embryogenesis (see below). In the absence of voucher specimens (Watabe, pers. comm.), we only speculate that their material from local pet shops (MEENAKSHI *et al.*, 1974) was the Brazilian *P. bridgesi* (Reeve, 1856), which is marketed commercially (THOMPSON, 1984; STARMÜHLNER, 1989).

Members of the Pilidae, Neritidae, and 36 families of pulmonates lay terrestrial eggs with calcified capsules (TOMPA, 1980). In reviewing available information on embryonic calcium dynamics in gastropods, TOMPA (1980) concluded that calcium for the hatchling is derived predominately from the capsule in cleidoic, calcified eggs and from extracapsular sources in non-cleidoic, poorly or uncalcified eggs. In *Anguispira alternata* (Say, 1816), the intracapsular contents at oviposition contain only 1% of the calcium of the 43-day embryo, and calcium content of the capsule is correspondingly reduced during embryogenesis (TOMPA, 1975). Only 6.7% of the calcium of the protoconch is attributable to the intracapsular fluids of *Pomacea* sp. (MEENAKSHI & WATABE, 1977). Hatchling *Veronicella ameghini* (Gambetta, 1923) derives 22% of its calcium from intracapsular fluids (TOMPA, 1980). In the present study, on the other hand, we found that embryonic calcium requirements of *P. paludosa* are met entirely from intracapsular sources. Without clear presentation of data or methodology, FOURNIÉ & CHÉTAIL (1984) indicated that *Deroceras reticulatum* (O. F. Müller, 1774) also is independent of capsular calcium; but BAYNE's (1966) equally brief account of a more qualitative analysis reported a reduction of capsular calcium.

TOMPA (1980) hypothesized that an osmotic or other toxic effect precluded the storage of sufficient intracapsular calcium to support embryogenesis of cleidoic eggs. But intracapsular calcium concentrations can be high in newly oviposited eggs: 3.8 mM in *Veronicella ameghini* (TOMPA, 1980); 9.1 mM in *Anguispira alternata* (calculated from TOMPA [1975]); 37 mM in *Deroceras reticulatum* (FOURNIÉ & CHÉTAIL, 1984); 183 mM in *Pomacea* sp. (calculated from MEENAKSHI *et al.* [1974: fig. 8] and MEENAKSHI &

WATABE [1977]); 745 mM in *Pomacea paludosa* (present study). Alternatively, FOURNIÉ & CHÉTAIL (1984) predicted that most of the calcium in intracapsular fluids is organically bound; this would seem to be the case for all species cited above if physiologic concentrations of free calcium are typically 10^{-3} mM (ECKERT *et al.*, 1988). The calcium-rich egg of *P. paludosa* represents an extreme in the range of strategies by which gastropods provide calcium for embryogenesis.

In addition to chemical analyses of capsules and intracapsular material, evidence for calcium resorption from the capsule comes from direct observation of changes in its crystalline structure. The number of calcium carbonate spherules in the partly calcified capsule of *Veronicella ameghini* decreases during embryogenesis (TOMPA, 1980). TOMPA (1979) demonstrated an observable loss of crystals in the capsule of *Stenotrema leaii* (Ward *in* Binney, 1840) and reported similar losses to occur in *Varohadra yeppoonensis* (Beddome, 1897) and *Helicodiscus parallelus* (Say, 1821). Heavy erosion of the initially thick inner crystalline layer in *Pomacea* sp. progresses to the thin, outer monolayer of spherules by the time of hatching (MEENAKSHI & WATABE, 1977). Erosion in *P. paludosa,* on the other hand, is superficial and does not contribute measurably to calcium dynamics of the embryo; changes in surface morphology and structural integrity of the inner capsular layer might only serve to weaken the capsule in preparation for hatching.

Reliance on eggshell calcium for embryogenesis has been demonstrated in insects (MOSCONA, 1948), gastropods (TOMPA, 1980), reptiles (PACKARD *et al.*, 1977), and birds (BOND *et al.*, 1988). The degree of reliance, however, varies widely. For example, embryos of altricial birds erode the eggshell mammillae less than do embryos of precocial birds (BOND *et al.*, 1988); and squamate reptiles rely on calcium stores in the yolk, whereas crocodilians and chelonians rely on eggshell calcium (PACKARD *et al.*, 1977). Mechanisms for calcium provision in terrestrial eggs of gastropods are more diverse (TOMPA, 1980) than for avian and reptilian eggs. The present study extends this diversity among gastropods further to include total reliance on calcium stores in the intracapsular fluids, a mechanism previously considered maladaptive (TOMPA, 1980).

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Ca-Binding Glycoproteins in Molluscan Shells with Different Types of Ultrastructure

by

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Abstract. Highly acidic Ca-binding glycoproteins were isolated from molluscan shells that have various types of ultrastructure. The molecular weights of the proteins were estimated to range between approximately 50,000 and 70,000 daltons and all were rich in acidic amino acids (particularly aspartate) and in glycine and serine. Based on the results of the amino acid analyses, Ca-binding glycoproteins could be classified into three major types: (1) those of the nacreous and prismatic layers; (2) those of the foliated and chalky layers; and (3) those of the homogeneous, composite-prismatic, complex, and crossed-lamellar layers.

INTRODUCTION

Molluscan shells consist primarily of crystals of calcium carbonate ($CaCO_3$), generally either aragonite or calcite. Depending on the arrangement of crystals, calcified layers of shells are classified into different types such as the granular, homogeneous, nacreous, prismatic, foliated, composite-prismatic, complex, and crossed-lamellar layers (MacClintock, 1967; Taylor *et al.*, 1969; Kobayashi, 1971; Carter, 1980; Carter & Clark, 1985; Uozumi & Suzuki, 1981). Small amounts of organic materials are also present in shells, as a periostracum, covering the outer surfaces of shells, and as an organic matrix in mineralized layers.

The organic matrix, which is a mixture of protein, glycoprotein, polysaccharide and lipid (Wada, 1964, 1980; Degens, 1979; Krampitz & Witt, 1979; Samata & Krampitz, 1981), is composed of two components: a water-soluble matrix (SM) and a water-insoluble matrix (ISM). A soluble matrix was first noted by Crenshaw (1972) in shells of *Mercenaria mercenaria*. Because of the Ca-binding capacity of the SM, it is considered essential for the process of shell formation. An insoluble matrix, which corresponds to "conchiolin" of Frémy (1855), constitutes the main part of the matrix and is thought to be the framework of the matrix. According to Grégoire (1972), the amino acid composition of the ISM differs among various taxa of mollusks. On the other hand, Akiyama (1966) and Kasai & Ohta (1981) found a more-or-less unique amino acid composition of the ISM for each type of shell ultrastructure, regardless of taxon. Moreover, Weiner (1983) fractionated the SM of the nacreous and prismatic layers of *Mytilus californianus* by HPLC and reported that the amino acid sequence of Asp-Pro-Thr-Asp is uniquely found in the calcitic prismatic layer. Although molecules in the organic matrix are considered to be laid down with a particular organization prior to the formation of crystals of $CaCO_3$, the origin and function of the organic matrix have not been clarified.

In the present study, amino acid compositions of the SM in various types of molluscan shell ultrastructures were determined, in order to correlate the composition, shell ultrastructure, and taxonomy of mollusks. For this purpose, the matrices were isolated from eight types of shell layers representing 11 molluscan families and three classes. After the Ca-binding components were fractionated from the bulk SM by two steps of column chromatography, the amino acid compositions of the Ca-binding components were compared.

MATERIALS AND METHODS

The taxonomies, localities of origin, and shell ultrastructures of the species examined are shown in Table 1.

Figure 1 shows a flow diagram of the preparation and analysis of the SM. After their surfaces were cleaned with a dental drill, shells were dipped in 1% NaClO to remove organic contaminants and periostracum. Individual layers of a shell were separated with a dental drill, dried, powdered, and decalcified. Decalcification was carried out in 1 N HCl and the salts were removed by dialysis against distilled water in Spectrapor No. 3 tubing (Spectrum Med-

Table 1

Taxonomic allocations, shell ultrastructures, and localities of origin of the 12 species examined. N, nacreous layer; P, prismatic layer; F, foliated layer; CH, chalky layer; H, homogeneous layer; CP, composite-prismatic layer; C, complex layer; CL, crossed-lamellar layer.

Taxonomy	Shell ultra-structure	Locality of origin
A. Gastropoda		
Haliotidae		
Haliotis discus Reeve	N, P	Sesoko Jima, Okinawa
Turbinidae		
Turbo cornutus Solander	N, P	Miura Shi, Kanagawa
B. Bivalvia		
Pteriidae		
Pinctada martensii Dünker	N, P	Omura Shi, Nagasaki
Pinnidae		
Atrina vexillum Born	N, P	Omura Shi, Nagasaki
Placunidae		
Placuna placenta Linné	F	Philippine
Pectinidae		
Patinopecten yessoensis Jay	F	Mutsu Shi, Aomori
Ostreidae		
Crassostrea gigas Thunberg	F, CH	Matsushima, Miyagi
Arcidae		
Anadara broughtonii Schrenck	C, CL	Misaki Shi, Kanagawa
Glycymeridae		
Glycymeris yessoensis Sowerby	C, CL	Mutsu Shi, Aomori
Veneridae		
Mercenaria stimpsoni Gould	H, CP	Georgetown, SC, USA
Meretrix lusoria Röding	H, CP	Kujukuri, Chiba
C. Cephalopoda		
Nautilidae		
Nautilus pompilius Linné	N, P	Kuro Shima, Okinawa

ical Industries Inc., New York, U.S.A.). Only molecules of molecular weight less than 3500 daltons passed through the pores of this dialysis tube. Each dialyzed sample was centrifuged (10,000 × g, 20 min). Only the supernatant was used for further fractionation.

An aliquot of 0.1 mL radioactive $^{45}CaCl_2$ (0.05 μCi) was added to each 2 mL of water-soluble sample before fractionation on a column of Bio-Gel A 1.5 m. Radioactivity was measured in a Packard Tricarb Model 4530 liquid scintillation counter (Packard Instrument Co., New York, U.S.A.).

The SM was initially loaded onto a 100 × 1.5 cm, Bio-Gel A 1.5 m column (Bio-Rad Laboratories, Tokyo, Japan), equilibrated with 0.1 M NH_4HCO_3, pH 8.4. The absorbance of the eluate was measured at 235 nm with a double beam spectrophotometer UV 150-02 (Shimazu Co., Kyoto, Japan). The Ca-binding fractions in the eluate were pooled, lyophilized, and subjected to ion exchange chromatography on a column (30 × 2.5 cm) of DEAE Sephacel (Pharmacia Japan Co., Tokyo, Japan), eluted with 0.1 M NH_4HCO_3 buffer and then with a linear gradient from 0 to 1 M NaCl in the same buffer. All fractions were pooled and desalted on a Bio-Gel P 6 column (50 × 0.9 cm), eluted with 0.01 M NH_4HCO_3. For precise determination of the molecular weight, material was run on columns of DEAE Sephacryl S-200 and Sephadex G 75 (Pharmacia Japan Co.; 100 × 1.5 cm), respectively, in the same buffer as used for chromatography on Bio-Gel A 1.5 m.

The purified Ca-binding fractions were hydrolyzed in a hydrolysis tube (Pierce Co., Chicago, U.S.A.) under vacuum, at 110°C for 24 h, in 6N HCl. The hydrolysates were then analyzed on an Atto MLC-703S automatic amino acid analyser (Atto Co., Tokyo, Japan).

Analysis was repeated for three Ca-binding fractions from different specimens of the same species.

SDS-Polyacrylamide gel electrophoresis was carried out in 12.5% gels as described by ANDERSON *et al.* (1983) and isoelectric focusing in ampholine (pH 3.0 to 10.0) as described by O'FARRELL (1975). Both gels were stained with 0.4% Coomassie Brilliant Blue R-250. Samples for electrophoresis were prepared in three concentrations (10, 50, and 100 μg/50 μL sample buffer).

Infrared spectroscopic analysis was performed by the diffuse reflectance method on an IR-810 DP 98 spectrophotometer (Japan Spectroscopic Co., Tokyo, Japan).

Quantitative analysis of phosphate was carried out by the method of TAUSSKY & SCHORR (1967) and of hexose by the method of SCHIELDS & BURNET (1960).
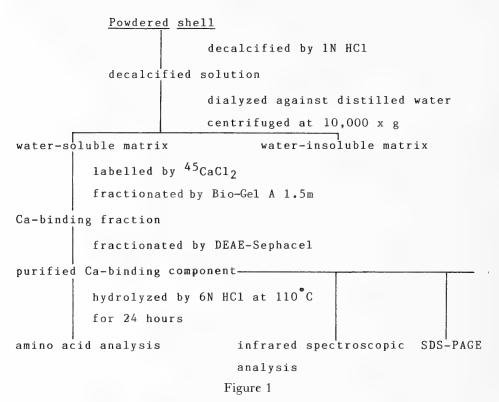
RESULTS

Total Amount of SM

The amount of SM was low, ranging from 0.01 to 0.2% of the total weight of each shell. The amount of the SM in the prismatic and foliated layers was the highest; the next highest level was found in the nacreous layer. The other four layers of shell had even lower amounts of SM.

Gel Chromatography

Elution profiles of SM obtained by Bio-Gel A 1.5 m are shown in Figure 2 (left). Sample species are *Pinctada martensii* for the nacreous and prismatic layers, *Crassostrea gigas* for the foliated layer, and *Glycymeris yessoensis* for the crossed-lamellar layer. Regardless of the type of ultrastructure, the largest amount of protein was eluted from the column with 60 to 90 mL of the buffer. This major fraction included about 70 to 80% of the total protein in

<u>Powdered shell</u>

decalcified by 1N HCl

decalcified solution

dialyzed against distilled water

centrifuged at 10,000 x g

water-soluble matrix   water-insoluble matrix

labelled by $^{45}CaCl_2$

fractionated by Bio-Gel A 1.5m

Ca-binding fraction

fractionated by DEAE-Sephacel

purified Ca-binding component

hydrolyzed by 6N HCl at 110°C

for 24 hours

amino acid analysis   infrared spectroscopic   SDS-PAGE

analysis

Figure 1

Flow-diagram of the procedure used for analysis of the water-soluble matrix.

the matrix and the eluted material had Ca-binding capacity. Rechromatography of the major protein fractions on DEAE Sephacryl S-200 and Sephadex G 75 showed essentially the same elution profiles for all species with major molecular weights ranging from about 50,000 to 70,000 daltons.

Ion Exchange Chromatography

Elution profiles after ion exchange chromatography (DEAE Sephacel) of the main components isolated by gel chromatography are shown in Figure 2 (right). The largest amount of protein was eluted by 0.5 to 0.6 M NaCl in the case of the prismatic, nacreous, and foliated layers, and at about 0.4 M NaCl in the case of the other four layers.

Ca-binding capacity could be detected only in the major acidic fractions of all species examined.

Amino Acid Composition
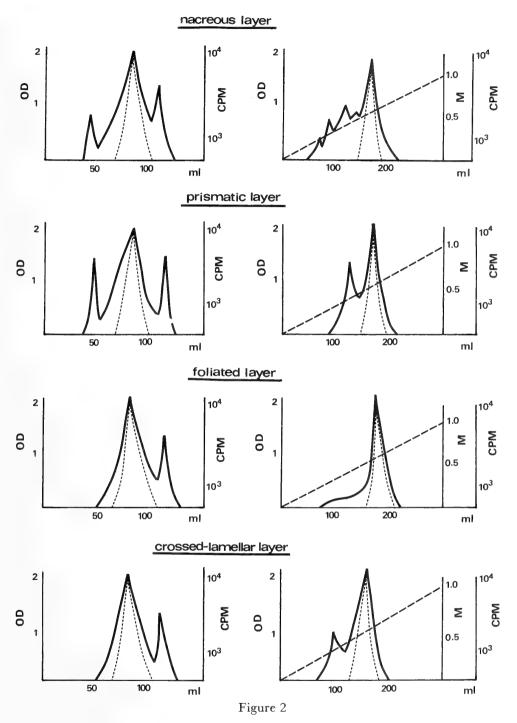
Amino acid compositions of the Ca-binding components in the nacreous and prismatic layers (Table 2), and in the foliated, chalky, homogeneous, composite-prismatic, complex, and crossed-lamellar layers (Table 3), are shown. The value for each amino acid corresponds to the mean value obtained from the analyses of three specimens for each species. Although some distinctive differences can be recognized in the amino acid compositions of shells of

different ultrastructures, the compositions were generally characterized by high levels of aspartate, glycine, glutamate, serine, and alanine. Acidic amino acids were found to be present at higher levels than basic amino acids. Polar amino acids were also present in high amounts.

Table 4 shows the mean value and the standard deviation of levels of each amino acid in the Ca-binding components isolated from the six shell layers examined. The mean value and the standard deviation were calculated for a total of five species in the case of both the nacreous and prismatic layers, three of the foliated layer, and two of the remaining three layers.

Compositions of the Ca-Binding Components in the Nacreous and Prismatic Layers

Although the nacreous layer is composed of aragonite, the prismatic layer is of calcite (in Gastropoda and Bivalvia) or aragonite (in Cephalopoda). As clearly indicated in Table 4, the range of variation of each amino acid (mean value + standard deviation) overlapped between the nacreous and prismatic layers for almost all amino acids. The values were somewhat different only in the case of alanine. This result shows the high degree of similarity in the amino acid composition of the Ca-binding components in the two ultrastructural layers. The composition was characterized by large amounts of aspartate and glycine, which com-

nacreous layer

prismatic layer

foliated layer

crossed-lamellar layer

Figure 2

Elution profiles of the water-soluble matrix in each shell layer obtained by Bio-Gel A 1.5 m (left) and DEAE Sephacel (right). Species: nacreous and prismatic layers, *Pinctada martensii*; foliated layer, *Crassostrea gigas*; crossed-lamellar layer, *Glycymeris yessoensis*. Key: -----, capacity of Ca-binding; - - -, concentration of NaCl; ——, absorbance at 235 nm. Absorbance at 235 nm (OD) is marked by the scale on the left margin of each profile; intensity of Ca-binding (CPM) and the salt gradient (M) is marked on the right margin of each profile.

Table 2

Amino acid compositions of the Ca-binding glycoproteins in the nacreous and prismatic layers (in molar percent). 1, *Haliotis discus*; 2, *Turbo cornutus*; 3, *Pictada martensii*; 4, *Atrina vexillum*; 5, *Nautilus pompilius*; 1 and 2 are gastropods, 3 and 4 are bivalves, and 5 is a cephalopod. —, not detected; a.a., amino acids.

Layer:	Nacreous					Prismatic				
Species:	1	2	3	4	5	1	2	3	4	5
Asx	26.55	27.46	26.38	26.79	29.23	29.53	26.40	28.95	28.55	25.58
Thr	3.44	5.70	3.12	5.13	3.31	2.95	3.72	3.03	4.81	3.33
Ser	6.22	7.30	6.48	8.15	4.98	8.00	9.15	10.75	9.09	3.96
Glx	8.87	9.72	10.73	9.56	9.44	8.41	11.27	9.42	10.59	9.55
Pro	6.81	6.62	6.24	4.24	6.17	4.82	5.40	5.10	5.14	5.01
Gly	22.48	15.41	23.15	19.55	17.75	25.46	17.63	21.54	17.99	18.68
Ala	6.47	7.58	6.58	5.95	7.40	4.10	3.96	5.28	5.81	2.56
Cys	0.81	0.21	1.06	1.46	0.50	0.50	1.98	1.29	0.63	—
Val	3.59	3.54	2.52	2.93	4.41	2.07	2.62	2.80	2.78	2.77
Met	1.46	1.26	0.20	0.85	0.33	—	—	0.13	—	0.42
Ile	1.66	2.00	1.27	1.68	2.66	0.81	1.62	1.56	1.91	1.99
Leu	3.29	3.95	2.84	2.84	4.89	2.29	2.98	3.55	3.34	2.60
Tyr	1.01	1.55	2.35	1.57	1.16	2.16	1.65	0.80	1.72	9.18
Phe	1.98	2.52	3.01	2.77	2.55	2.44	3.83	1.46	2.24	3.00
Lys	3.76	2.19	1.80	2.62	1.81	3.14	2.62	1.33	2.07	5.49
His	0.40	1.00	0.43	1.21	1.02	0.57	1.84	0.96	1.47	2.21
Arg	2.82	1.78	1.84	2.70	2.39	2.75	3.33	2.05	1.86	3.67
Acidic a.a.	35.42	37.18	37.11	36.35	38.67	37.98	37.67	38.37	39.14	35.13
Basic a.a.	6.98	4.97	4.07	6.53	5.22	6.46	7.79	4.34	5.40	11.37
Acidic/basic	5.07	7.48	9.12	5.57	7.41	5.88	4.84	8.84	7.25	3.09
Asx/Glx	2.99	2.83	2.46	2.80	3.10	3.51	2.34	3.07	2.70	2.68
Hydroxy a.a.	9.66	13.00	9.60	13.28	8.29	10.95	12.87	13.78	13.90	7.29
Ser/Thr	1.81	1.28	2.08	1.59	1.50	2.71	2.46	3.55	1.89	1.19
Gly/Ala	3.47	2.03	3.52	3.29	2.40	6.21	4.45	4.08	3.10	7.30
Asx/Gly	1.18	1.78	1.14	1.37	1.65	1.26	1.50	1.34	1.59	1.37
Polar a.a.	75.36	72.32	77.34	78.74	71.59	83.51	79.61	80.12	78.78	81.65

prised from 26 to 30 mole percent (%) for aspartate and 15 to 25% for glycine. The level of glutamate was also high, being about 10% or 40% higher than in the foliated layer. Among the hydroxy amino acids, serine was lower in concentration and threonine higher in the nacreous and prismatic layers than in the foliated layer. Acidic amino acids were present at higher levels than basic amino acids in both layers. Proline, which was present in only small amounts in the foliated layer, was found at concentrations about 2- to 3-fold greater in the nacreous and prismatic layers. Apart from these amino acids, the amounts of valine, isoleucine, leucine, phenylalanine, lysine, and histidine were slightly higher than in the foliated layer. Among aromatic amino acids, phenylalanine was usually present in higher levels than tyrosine, but this trend was reversed in the foliated layer.

For a more precise comparison between the nacreous and prismatic layers, the ratio of each amino acid residue in the Ca-binding components in the nacreous layer to that in the prismatic layer was calculated for five species. The results show a distinct increase in the amount of alanine and a decrease in the amount of histidine and of polar amino acids in the nacreous layer as compared to the

prismatic layer. Moreover, serine residues were more concentrated in the prismatic layer. These trends were found in almost all the species examined.

In contrast to the similar compositions of the Ca-binding components of the specimens of Gastropoda and Bivalvia, the composition of the cephalopod *Nautilus pompilius* was unique with respect to several amino acids. In particular, the level of serine was low, about 25% lower in the nacreous layer and 50% lower in the prismatic layer than in the other species. Moreover, the extremely low level of alanine, the high levels of tyrosine and lysine, and the low ratio of serine to threonine were also characteristic of the prismatic layer of this species. The unique composition of *N. Pompilius* is in large measure responsible for the high value of the standard deviations of serine, tyrosine, and lysine for the prismatic layer of the five species examined (see Table 4).

Compositions of the Ca-Binding Components in the Foliated and Chalky Layers

The amino acid compositions of the Ca-binding components in the calcitic foliated and chalky layers were similar, characterized by high levels of aspartate, serine,

Table 3

Amino acid compositions of the Ca-binding glycoproteins in the foliated, chalky, homogeneous, composite-prismatic, complex, and crossed-lamellar layers (in molar percent). 6, *Placuna placenta*; 7, *Patinopecten yessoensis*; 8, *Crassostrea gigas*; 9, *Mercenaria stimpsoni*; 10, *Meretrix lusoria*; 11, *Anadara broughtonii*; 12, *Glycymeris yessoensis*; all are bivalves. —, not detected; a.a., amino acids.

Layer:	Foliated			Chalky	Homogeneous		Composite-prismatic		Complex		Crossed-lamellar	
Species:	6	7	8	8	9	10	9	10	11	12	11	12
Asx	19.50	26.92	32.65	31.85	12.55	14.67	16.50	18.93	11.86	12.21	10.86	12.24
Thr	1.38	2.11	2.26	2.16	7.88	7.20	7.89	6.83	4.62	5.75	5.06	5.30
Ser	20.37	18.12	16.75	19.44	8.82	6.95	7.79	8.00	5.40	5.90	5.33	5.36
Glx	4.86	6.16	5.97	6.02	11.25	10.13	12.46	10.50	9.49	10.66	11.28	11.66
Pro	1.34	2.86	1.24	1.37	8.71	9.33	10.39	8.87	17.34	16.61	15.85	13.82
Gly	32.80	26.24	27.37	26.33	9.45	9.85	13.36	13.50	16.09	13.63	15.67	12.68
Ala	5.54	7.43	4.59	3.84	6.70	5.57	8.47	7.24	12.68	11.47	12.02	10.35
Cys	0.14	0.42	1.26	1.06	1.51	2.02	1.14	0.88	0.22	1.25	0.60	0.96
Val	1.61	0.97	0.88	0.87	5.74	4.62	3.90	4.54	4.90	4.46	5.03	5.35
Met	—	—	—	—	0.57	1.09	0.25	—	0.44	0.11	0.62	0.74
Ile	0.48	0.25	0.23	0.55	3.44	3.64	1.88	3.00	2.93	2.73	2.94	3.80
Leu	1.80	2.82	1.50	1.18	4.05	3.83	4.12	4.31	4.52	3.97	4.97	5.11
Tyr	3.05	1.44	2.59	2.61	3.03	3.42	2.58	2.00	0.95	0.91	0.07	1.03
Phe	0.84	0.51	0.18	0.90	2.61	4.00	2.04	2.50	2.31	3.00	2.56	3.01
Lys	0.84	1.63	1.10	0.85	7.53	8.38	4.75	5.10	2.88	4.27	3.16	4.43
His	0.41	0.31	0.25	0.09	3.84	2.40	1.10	1.30	0.87	0.85	0.53	0.67
Arg	3.54	1.81	1.18	0.88	2.32	2.88	1.38	2.56	2.52	2.22	3.44	3.49
Acidic a.a.	24.36	33.08	38.62	37.89	23.80	24.80	28.96	29.43	21.35	22.87	22.14	23.90
Basic a.a.	4.97	3.75	2.53	1.82	13.69	13.66	7.23	8.96	6.27	7.34	7.13	8.59
Acidic/basic	5.09	8.82	15.26	20.82	1.74	1.82	4.01	3.28	3.41	3.12	3.11	2.78
Asx/Glx	4.01	4.37	5.47	5.29	1.12	1.45	1.32	1.80	1.25	1.15	0.96	1.05
Hydroxy a.a.	21.75	20.23	19.01	21.60	16.70	14.15	15.68	14.83	10.02	11.65	10.39	10.66
Ser/Thr	14.76	8.59	7.41	9.00	1.12	0.97	0.99	1.17	1.17	1.03	1.05	1.01
Gly/Ala	5.92	3.53	5.96	6.86	1.41	1.77	1.58	1.86	1.27	1.19	1.30	1.23
Asx/Gly	0.59	1.03	1.19	1.21	1.33	1.49	1.24	1.40	0.74	0.90	0.69	0.97
Polar a.a.	86.89	85.16	91.38	91.31	68.18	67.90	68.95	70.18	54.90	57.65	56.00	57.82

and glycine, which constituted 70 to 80% of the total amino acid residues. In particular, the level of serine was 2- to 4-fold greater than in the remaining shell layers. As a result of such high proportions of these three amino acids, polar amino acids together represented about 85 to 91% of total residues. Moreover, the ratios of acidic to basic amino acids and of serine to threonine were also characteristically high. Of the other amino acids eluting after alanine from the column, cystein, isoleucine, phenylalanine, lysine, and histidine were found, but only in very small amounts.

The amounts of aspartate, serine, and glycine varied in the three species examined. Aspartate was found at its highest level in *Crassostrea gigas* and at its lowest in *Placuna placenta*, while the highest levels of serine and glycine were found in the latter species.

The standard deviation of levels of aspartate among the three species was 2-fold greater than the value among the three specimens of each species. In addition, the standard deviation in the levels of aspartate among the three species was also slightly greater than those in the levels of serine and glycine.

Compositions of the Ca-Binding Components in the Homogeneous, Composite-Prismatic, Complex, and Crossed-Lamellar Layers

The amino acid compositions of the Ca-binding components in these four shell layers of aragonite were different from those of the nacreous, prismatic, foliated, and chalky layers, in terms of the greater levels of proline and smaller levels of aspartate, glycine, and polar amino acids. These aragonitic layers also had lower ratios of aspartate to glutamate, serine to threonine, and glycine to alanine.

The amino acid compositions were very similar in the two species with shells of the same ultrastructure, in contrast to the differences between the homogeneous and composite-prismatic, and the complex and crossed-lamellar layers (Tables 3, 4). Although the compositions of the latter pair of layers were very similar, slight differences were detected between the former pair.

The homogeneous and composite-prismatic layers of both *Mercenaria stimpsoni* and *Meretrix lusoria* contained higher amounts of aspartate and hydroxy amino acids and lower amounts of proline and alanine, combined with higher

Table 4

Mean value and standard deviation of levels of each amino acid in the Ca-binding components in the six shell layers.
Values are calculated for a total of five species in the case of both the nacreous and primsatic layers, three for the foliated,
and two for the remaining three layers. —, not detected or not calculated.

	Nacreous		Prismatic		Foliated		Homogeneous		Composite-prismatic		Crossed-lamellar	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Asx	27.28	1.04	27.80	1.53	26.36	5.38	13.36	1.31	17.72	1.22	11.79	0.56
Thr	4.14	1.06	3.57	0.68	1.92	0.38	7.54	0.34	7.36	0.53	5.18	0.41
Ser	6.63	1.07	8.19	2.29	18.41	1.49	7.89	0.94	7.90	0.11	5.50	0.23
Glx	9.66	0.61	9.85	0.99	5.66	0.57	10.69	0.56	11.48	0.98	10.77	0.82
Pro	6.02	0.92	5.09	0.19	1.81	0.74	9.05	0.31	9.63	0.76	15.91	1.31
Gly	19.67	2.89	20.26	2.94	28.80	2.86	9.65	0.20	13.43	0.07	14.52	1.41
Ala	6.80	0.61	4.34	1.13	5.85	1.18	6.14	0.57	7.86	0.62	11.63	0.86
Cys	0.81	0.49	0.88	0.56	0.61	0.48	1.77	0.26	1.01	0.13	0.76	0.39
Val	3.40	0.64	2.61	0.28	1.15	0.33	5.18	0.56	4.22	0.32	4.94	0.32
Met	0.82	0.50	—[b]	—	—	—	0.83	0.26	0.13	0.08	0.48	0.24
Ile	1.85	0.46	1.58	0.42	0.32	0.11	3.54	0.10	2.44	0.56	3.10	0.41
Leu	3.56	0.78	2.95	0.46	2.04	0.56	3.95	0.10	4.22	0.10	4.64	0.45
Tyr	1.53	0.47	3.10	3.07	2.36	0.68	3.23	0.20	2.29	0.29	0.74	0.39
Phe	2.57	0.34	2.59	0.79	0.51	0.27	3.31	0.70	2.27	0.23	2.72	0.30
Lys	2.44	0.73	2.93	1.41	1.19	0.33	7.96	0.43	4.93	0.18	3.69	0.67
His	0.81	0.33	1.41	0.59	0.32	0.07	3.37	0.97	1.20	0.10	1.49	1.10
Arg	2.31	0.43	2.73	0.70	2.18	1.00	2.60	0.28	1.94	0.56	2.92	0.56

ratios of aspartate to glutamate, glycine to alanine, and aspartate to glycine than were found in the complex and crossed-lamellar layers. Between the homogeneous and composite-prismatic shell layers, differences were apparent in the amounts of aspartate, glycine and alanine, which were concentrated in the composite-prismatic layer, and in the proportions of aromatic and basic amino acids, which were concentrated in the homogeneous layer. The compositions of the Ca-binding components in the complex and crossed-lamellar layers of *Glycymeris yessoensis* and *Anadara broughtonii* were very similar to one another. Proline was the most abundant residue, accounting for nearly 14% or more of the total amino acid residues in each layer. Next in abundance was glycine, comprising about 13 to 16% of the total, followed by alanine, serine, tyrosine, and polar amino acids. Ratios of glycine to alanine, and of aspartate to glycine, were lower in the complex and the crossed-lamellar layers than in the Ca-binding components in the other layers.

SDS-Polyacrylamide Gel Electrophoresis and Isoelectric focusing

The Ca-binding components from each shell layer were subjected to SDS-Polyacrylamide gel electrophoresis and isoelectric focusing. No bands were observed after staining by Coomassie Brilliant Blue, regardless of sample concentration.

Infrared Spectroscopic Analysis

The infrared spectrum of the Ca-binding components in the nacreous layer of *Turbo cornutus* is shown in Figure

3. Peaks are seen at the position of 3280 cm^{-1}, 3070 cm^{-1}, 1658 cm^{-1}, 1534 cm^{-1}, 1230 cm^{-1}, 700 cm^{-1}, and 610 cm^{-1}. The absorptions at 3280 cm^{-1}, 3070 cm^{-1}, 1658 cm^{-1}, 700 cm^{-1}, and 610 cm^{-1} correspond to those of Amides A, B, I, and IV, respectively. However, one cannot determine whether the absorptions at 1534 cm^{-1} and 1230 cm^{-1} are those of Amide II and III or of carbohydrate. Additional peaks were seen at the positions of 1080 cm^{-1} and 890 cm^{-1} and might be due to absorbance by carbohydrates.
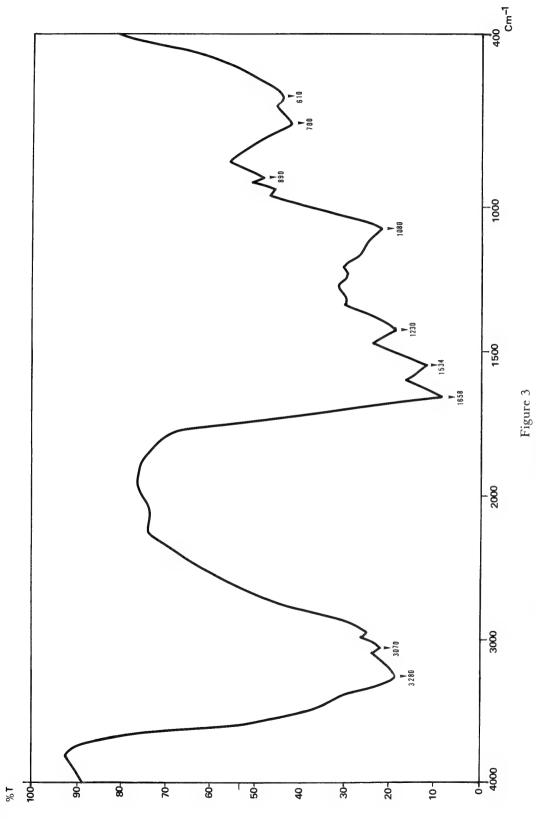
Quantitative Analysis of Phosphate and Hexose

Only trace amounts of phosphate were detected from all the samples examined. The amount of hexose was 2 to 3.5% (by weight) in the samples of the nacreous and foliated layers, and 0.5 to 1% of the remaining shell layers.

DISCUSSION

Ca-binding components were isolated from all the specimens examined. Although amino acid analysis showed that their main constituents were acidic amino acids, the exact isoelectric points of the Ca-binding components have not yet been determined because of the problem in staining gels after isoelectrofocusing. The data from the infrared spectroscopic analysis combined with the data from the quantitative analysis of hexose also demonstrated carbohydrates in the Ca-binding components. These results indicate that the Ca-binding components are composed primarily of highly acidic glycoproteins.

Gel exclusion chromatography indicated that the size of the Ca-binding glycoprotein was in the range of 50,000 to

Figure 3

Infrared spectrum of the Ca-binding glycoproteins in the nacreous layer of *Turbo cornutus*.

70,000 daltons. Although WEINER et al. (1977), using SDS-polyacrylamide gel electrophoresis, showed the presence of components with discrete molecular weights in the SM of several molluscan species, no visible bands could be detected by Coomassie Blue staining in the present study. The lack of detection may be due to the low proportion of basic amino acids in the glycoprotein or to some co-existing carbohydrate moiety; more suitable conditions for electrophoresis and staining must be found in the future. Although the purity of the glycoproteins could not be checked electrophoretically, further fractionation of the Ca-binding components was impossible, at least by column chromatography. The highly acidic nature of the components was also clearly shown by chromatography on DEAE Sephacel: components could be released from the anion exchange resin only at the high ionic strength of 0.4 to 0.6 M NaCl. In previous studies, heterogeneous components were identified in the SM by ion exchange chromatography, by adjusting the concentrations of NaCl (usually less than 0.3 M) at which the proteins eluted (WEINER, 1979; WEINER et al., 1977). The detection of components at lower ionic strength than in the present study could result from the binding of EDTA to the protein. This possibility cannot be ruled out, since a large quantity of EDTA may still remain after gel chromatography (SAMATA & MATSUDA, 1986).[1]

In spite of the high degree of similarity in the behavior of the Ca-binding components during column chromatography, the amino acid composition of the components varied primarily according to the ultrastructures of the shells. The samples used for this analysis included 12 species of three orders of Mollusca, which were composed of eight types of shell ultrastructure. The compositions of the Ca-binding glycoproteins in both the nacreous and prismatic layers of five species of Gastropoda and Bivalvia were very similar, despite their widely separated taxonomic positions. On the contrary, the Ca-binding glycoproteins of nine species of Bivalvia, whose shells are composed of eight types of ultrastructure, had unique compositions according to the ultrastructure. Moreover, the compositions of the
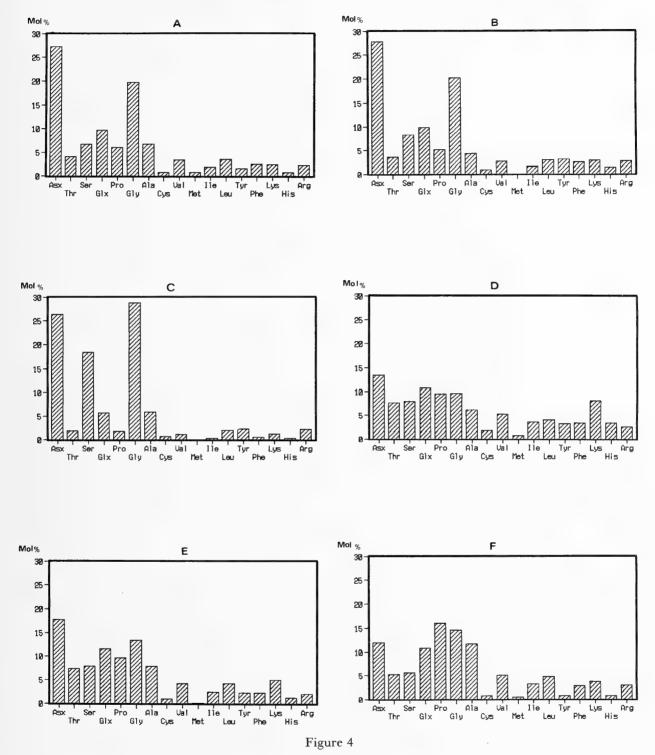
Ca-binding glycoproteins in the homogeneous and composite-prismatic layers differed from each other. These data imply that the composition of the Ca-binding glycoproteins may vary primarily according to shell ultrastructure, and not to taxonomic position.

Based on the amino acid composition, the Ca-binding glycoproteins can be classified into three types: (1) those of the nacreous and prismatic layers; (2) those of the foliated and chalky layers; and (3) those of the remaining four shell layers. These three types differ primarily with respect to the amounts of aspartate, serine, proline, glycine, and alanine (Figure 4). The amounts of threonine, glutamate, and lysine also vary but to a lesser extent. Almost all other amino acids, whose levels were relatively low, showed slight variations according to shell ultrastructure. In the third type of ultrastructure, two additional subtypes can be distinguished between the homogeneous and composite-prismatic layers, and the complex and crossed-lamellar layers. The difference was most remarkable in terms of the amounts of proline, tyrosine, and hydroxy amino acids. Moreover, the compositions of the Ca-binding glycoproteins differ slightly, in terms of the amounts of aspartate, glycine, alanine, and basic amino acids, between the homogeneous and composite-prismatic layer (Figure 4).

Amino acid analyses by previous workers have been carried out mainly on the unfractionated ISM regardless of ultrastructure. Therefore, the previous results are not comparable to those obtained for the Ca-binding glycoproteins in the present study. For example, MEENAKSHI et al. (1971) found the ISM in the nacreous layer to be rich in glycine and alanine, in contrast to the high levels of aspartate of the Ca-binding glycoprotein in the same layer.

The organic matrix has been suggested to be responsible for initiating, regulating, and limiting mineral growth (WEINER & HOOD, 1975; KRAMPITZ et al., 1976; WHEELER et al., 1988). For understanding the function of the matrix, interactions between the SM and the ISM must be elucidated. SAMATA (1988a) indicated the distinctive difference in composition between the SM and the ISM of both the nacreous and prismatic layers. Moreover, the composition of the ISM was also far separated between the two layers. On the other hand, the compositions of the two matrices were very close in other shell layers (SAMATA, 1988b). Thus, the organic matrix may participate in calcification in different ways between these two groups of shell ultrastructures, i.e., the nacreous and prismatic layers and the remaining six layers. In the nacreous and prismatic layers, the ISM may limit crystal growth, and thus regulate the orientation of crystals to the arrangement of the nacreous and prismatic layers, because the amino acid compositions of the Ca-binding glycoproteins in the SM did not differ significantly. Whether the Ca-binding glycoproteins in these layers play a positive role, such as transporting Ca-ions or initiating crystal nuclei, or serve as a

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[1] In the present study, HCl was used for decalcification of molluscan shells in order to avoid contamination that may occur by the use of EDTA. Although dilute acid could introduce cleavage in peptide bonds and denaturation in protein structure, KASAI & OHTA (1981) reported that the amino acid composition of the matrix varied little when shells were decalcified by EDTA or dilute acids. In addition, high capacity of Ca-binding could still be detected in matrix that was decalcified by HCl (SAMATA, 1988a). These results imply that organic matrix in molluscan shells is fairly resistant to acids. Furthermore, the use of EDTA has certain disadvantages. EDTA binds tightly to the inner wall of dialysis tubing, and also forms unidentifiable biopolymers with proteins, which are difficult to separate (SAMATA & MATSUDA, 1986). All the common amino acids are present in EDTA of special grade (Wako Pure Chemicals, Osaka, Japan) in amounts that cannot be ignored and EDTA ia also capable of binding Ca^{2+}-ions (SAMATA & MATSUDA, 1986).

Figure 4

Diagrams of the amino acid compositions of the Ca-binding glycoproteins in six different shell layers. A. Amino acid compositions of the Ca-binding glycoproteins in the nacreous layer of *Pinctada martensii*. B. Amino acid compositions of the Ca-binding glycoproteins in the prismatic layer of *Pinctada martensii*. C. Amino acid compositions of the Ca-binding glycoproteins in the foliated layer of *Crassostrea gigas*. D. Amino acid compositions of the Ca-binding glycoproteins in the homogeneous layer of *Meretrix lusoria*. E. Amino acid compositions of the Ca-binding glycoproteins in composite-prismatic layer of *Meretrix lusoria*. F. Amino acid compositions of the Ca-binding glycoproteins in the complex and crossed-lamellar layers of *Glycymeris yessoensis*.

limiting factor for the crystal growth cannot now be determined.

Because aspartic acid is usually the most abundant residue in the SM of several kinds of molluscan shells (CRENSHAW, 1972; WEINER & HOOD, 1975; WEINER, 1979; NAKAHARA et al., 1982), this acidic amino acid has been assumed to be one of the most important components involved in shell formation. WEINER (1979) and WEINER & TRAUB (1981) suggested that the SM may form a two-dimensional sheet with regularly spaced carboxyl groups of aspartic acids on the surface. This precise spatial arrangement of the carboxyl-groups may react with Ca^{2+} ions and promote the nucleation of crystals of $CaCO_3$. DEGENS (1979) presented a similar idea in relation to the role of the SM. As in the previous data, which were based on the measurements made on the unfractionated matrix, aspartate was usually the most abundant residue in the purified Ca-binding glycoproteins, except in the complex and crossed-lamellar layers. However, the amount of aspartate showed distinctive variations according to the ultrastructure of the shell. The most distinctive difference was between the nacreous and prismatic layers, and the homogeneous, composite-prismatic, complex, and crossed-lamellar layers. This result could imply different functions of the glycoproteins in the process of shell formation. In the foliated and chalky layers, aspartate was present in high amounts but serine was also highly concentrated. Serine is generally recognized to be present mostly as phosphoserine (BUTLER, 1987). WHEELER et al. (1988) demonstrated that such phosphorylation of the matrix may be significant for regulating the morphology of carbonate. The amino acid compositions of the organic matrix may also depend on various environmental factors to which mollusks are subjected. From the results of a comparative analysis on the unfractionated matrix, DEGENS et al. (1967) showed that amino acid compositions of the matrix are correlated with environmental factors. DUSSART (1984) also reported that the amino acid compositions of the shells of 13 species of freshwater Bivalvia reflected phylogenetic affinity but that environmental factors were probably important. Samata (unpublished data) has also pointed out the slight difference in the amino acid compositions of the Ca-binding glycoproteins in the nacreous and prismatic layers between the marine and freshwater species of Bivalvia. The difference was most remarkable with respect to the levels of aspartate.

The compositions of the Ca-binding glycoproteins in the nacreous and prismatic layers of Nautilus pompilius were slightly different from those in the same layers of the species of Gastropoda and Bivalvia, and also from those in the other shell layers. Nautilus is distributed in fairly deep waters in tropical seas, whereas the other species examined are restricted to shallow waters. The unique habitat of Nautilus makes it difficult to determine whether the difference in amino acid composition can be accounted for by environmental or phylogenetic factors.

The amino acid composition of the Ca-binding glycoprotein in the composite-prismatic layer was clearly different from those of the nacreous, prismatic, and foliated layers. The composite-prismatic layer was first defined by BøGGILD (1930) and has been considered to be a subdivision of the prismatic layer by some later investigators (CARTER, 1980; UOZUMI & SUZUKI, 1981). KOBAYASHI (1968) noted that the ISM in this layer resembled that in the complex and crossed-lamellar layers both morphologically and histochemically, but differed from that in the nacreous and prismatic layers. Moreover, because the mollusks that contain this layer are taxonomically close to those that contain the homogenous, complex, and crossed-lamellar layers, the composite-prismatic layer may be closely related to these three shell layers.

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A New Species of the Genus *Cyerce* Bergh, 1871, from the Cape Verde Islands (Opisthobranchia: Ascoglossa)

by

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Abstract. *Cyerce* **verdensis** Ortea & Templado, sp. nov., is described from the Cape Verde Islands (eastern Atlantic). The presence of papillae on the rhinophores, pericardium, and cerata is the main differential feature of this new species. The Atlantic species of the genus Cyerce are listed and discussed.

INTRODUCTION

In a recent paper (ORTEA & TEMPLADO, 1988) a new species from Cuba, *Cyerce habanensis,* was described, and the Atlantic species of this genus were discussed. At the same time, THOMPSON (1988) described another new species of this genus from the Saronic Gulf, *C. graeca,* in one of his works on eastern Mediterranean opisthobranchs. Following his advice on the necessity of further studies on this genus, we describe here another new species of *Cyerce* from the tropical eastern Atlantic, collected during the "Primera Expedición Científica Ibérica al Archipiélago de Cabo Verde" (August of 1985).

Family CALIPHYLLIDAE Thiele, 1931

Genus *Cyerce* Bergh, 1871
= *Lobifera* Pease, 1866
= *Lobiancoia* Trinchese, 1881

Cyerce verdensis Ortea & Templado, sp. nov.

(Figures 1–3)

Material: One specimen (Figures 1–3), 16 mm in length (18 August 1985), and four others 13, 12, 10, and 5 mm in length (20 August 1985), all collected between 0 and 2 m deep on *Halimeda* sp., in Salamança Bay (16°54′N, 24°57′W), San Vicente Island, Cape Verde Archipelago.

The largest specimen has been chosen as holotype, and deposited in the Museo Insular de Ciencias Naturales, Tenerife, Canary Islands (catalogue number MO/0092). The four paratypes are in the malacological collection of the Museo Nacional de Ciencias Naturales de Madrid, Spain (catalogue number 15.05/1033).

Etymology: Named after the Cape Verde Islands.

Description: The general body color of the animal is pale ochre. The dark brown digestive gland, which can be discerned clearly through the skin, is divided into two main branches that almost reach the posterior part of the dorsum. Each branch ramifies towards the cerata, without extending into them (Figure 1).

The foot is light in color, almost semi-translucent. Its frontal margin is rounded and a transverse mesopodial groove is present in the anterior one-third (Figure 2A).

The brownish pericardium has granulose white papillae. Such small papillae are present all over the dorsum. The bulky anal papilla is situated just before the pericardium, somewhat to the right of the median plane.

The rhinophores are split and inrolled. They have a disperse, brown and white pigmentation. Granulose papillae of a pale creme color are present on their distal half. The oral tentacles, also inrolled, are translucent with some white dots.

The leaf-shaped cerata are translucent with their distal margins angulose owing to some small white granules. Papillae, white granules, and superficial red-brown specks are present on both sides of the cerata (Figure 2B, C).

The radula of the 16-mm long specimen has 10 teeth in the ascending series and 13 in the descending one. The ascus contains more than 100 cluttered teeth. The functional teeth reach up to 80 μm in length at the beginning of the descending series. They are elongate and exhibit 12 denticles on both cutting edges. The protuded median zone of each tooth has two blunt protuberances (Figure 3B).

The penis is armored with a small nail-like spine that measures 10 μm in length (Figure 3A).

Discussion: In a former paper (ORTEA & TEMPLADO, 1988) we have already discussed the Atlantic species of this genus. *Cyerce verdensis* clearly differs from all these by the presence of granulose papillae all over the dorsum, rhinophores, and cerata. Such papillae are lacking in the other species. The disposition of the papillae in the cerata resembles *Polybranchia viridis* (Deshayes, 1857), previously collected in the Canary Islands (ORTEA, 1981). This latter species reaches 55–70 mm in length, and its juveniles are easily confused with *C. verdensis* at first sight. However, *P. viridis* lacks a transverse mesopodial groove and the diverticula of the digestive gland extend into the cerata.

The radular teeth of *Cyerce verdensis* are shorter and wider in proportion compared to those of *C. cristallina* and *C. antillensis,* and similar to those of *C. graeca* and *C. habanensis.*

Cyerce edmundsi Thompson, 1977, from Jamaica, also exhibits some pearl-like white glands in the distal margin of the ceras. However, the lack of a transverse mesopodial groove and the diverticula of the digestive gland in the cerata suggests that it belongs to another genus. MARCUS (1982) and JENSEN & CLARK (1983) commented that *C. edmundsi* could be a junior synonym of *Mourgona germainae* Marcus & Marcus, 1970.

The fact that all the specimens of *Cyerce verdensis* were found on the chlorophyte *Halimeda* sp. suggests that this seaweed constitutes its food. We previously reported another species of this genus, *Halimeda opuntia*, as the probable food of *C. habanensis* (ORTEA & TEMPLADO, 1988).

Including the present paper, the Atlantic (including Mediterranean Sea) species of the genus *Cyerce* are the following:

—*C. cristallina* (Trinchese, 1881). Mediterranean and Caribbean Sea.
—*C. antillensis* Engel, 1927. Caribbean region.
—*C. graeca* Thompson, 1988. Eastern Mediterranean (known from the Saronic Gulf only).
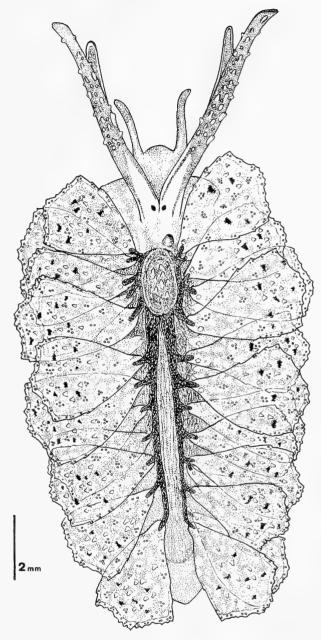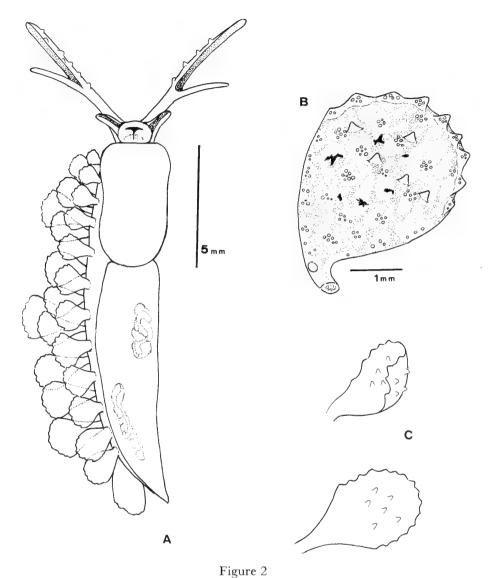
Figure 1

Cyerce verdensis Ortea & Templado, sp. nov., dorsal view of holotype.

—*C. habanensis* Ortea & Templado, 1988. Caribbean region (known from northern Cuba only, but the species cited by MARCUS & HUGHES (1974) as *C. antillensis* in Barbados might be this species).
—*C. verdensis* sp. nov. Cape Verde Islands (eastern Atlantic).
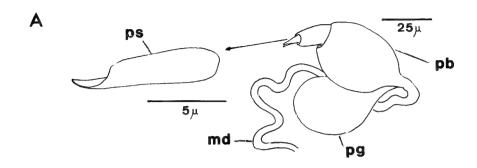
This last species is the first one of the genus which has been recorded from the eastern Atlantic Basin outside of the Mediterranean Sea.

Figure 2
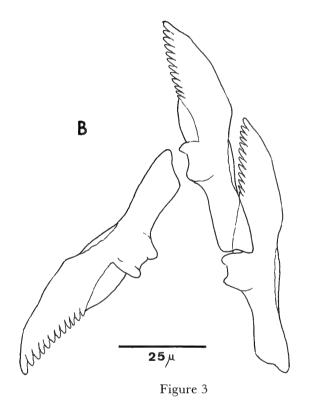
Cyerce **verdensis** sp. nov. A, ventral view; B and C, details of the cerata.

Figure 3

Cyerce **verdensis** sp. nov. A, terminal part of the male reproductive system showing the nail-like penial stylet; B, radular teeth. md, male duct; pb, penial bulb; pg, prostatic gland; ps, penial stylet.

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31 August–6 September 1986

edited by W. F. Ponder. Assoc. eds. D. J. Eernisse & J. H. Waterhouse. *Malacological Review.* Supplement 4:1–346.

Prosobranch gastropod phylogeny is in a state of dynamic flux, and no work demonstrates this more strikingly than the present volume. Much of the revolutionary change that is taking place in molluscan systematics is a direct result of the widespread acceptance of cladistics as a phylogenetic tool, along with the discovery of several important new taxa and additional characters. Two tenets of cladistics are responsible for necessitating fundamental changes in gastropod systematics. First, phylogenetic relationships should be determined on the basis of shared advanced (apomorphic) characteristics not primitive ones (plesiomorphies). Secondly, all taxa must be monophyletic. This means that all groups must share the most recent common ancestor and include all of the descendants of that ancestor. Any other arrangement is either polyphyletic or paraphyletic and is not permissible under cladistic doctrine. Paraphyletic taxa, where some, but not all of the descendants of a common ancestor are included in a group, are the most problematic in systematics. This is a problem because so many of our traditional taxonomic groups fall into this category. For example, invertebrates are paraphyletic since they exclude vertebrates, which are derived from invertebrate ancestors. Similarly, archaeogastropods are paraphyletic and perhaps even polyphyletic.

The relationships within the group traditionally referred to as the Archaeogastropoda is a major focus of several of the papers contained in this volume. This issue is discussed at length by Hickman and Haszprunar, although the latter author prefers to retain the Archaeogastropoda as a paraphyletic taxon. Unfortunately, owing to the publication time Haszprunar's "preliminary work" actually appeared after his more comprehensive work on the phylogeny of the Streptoneura published in the *Journal of Molluscan Studies.* Incidentally, both Streptoneura and Prosobranchia must be regarded as paraphyletic taxa, as well. Lindberg has demonstrated that convergence is rampant in patellogastropods particularly relative to shell shape and radular morphology, but that shell microstructure and modification of respiratory structures are excellent indicators of monophyly. The papers of McLean and Haszprunar, dealing with hydrothermal vent limpets and cocculiniform gastropods, demonstrate that increased exploration has revolutionized molluscan systematics as much as new

methods of interpreting relationships. The addition of many new higher taxa of limpets will certainly require a fundamental reassessment of gastropod origins and phylogeny.

Other major phylogenetic works contained in this volume include Houbrick's detailed phylogenetic analysis of the Cerithioidean gastropods, Ponder's preliminary study of truncatelloidean radiations, and Taylor & Morris' phylogeny of neogastropods. Our understanding of all three of these groups of highly derived gastropods is greatly enhanced by these contributions.

Several contributions clarify the phylogeny or systematics within smaller taxonomic groups. The most significant is Bieler's work on the Architectonicidae, which has implications to another major controversial area in gastropod phylogeny, the relationship of the Heterogastropoda and the Euthyneura (Opisthobranchia + Pulmonata). Rath's work on the Valvatidae also has implications to this controversy, though her conclusions seem to be based exclusively on ctenidial structure. There are clearly major disagreements in what constitutes homology and primary and secondary structures in gastropod gills; this issue requires considerable more attention and discussion. Luque, Templado & Burnay provide a short but well executed paper clarifying some aspects of litiopid systematics.

Five other papers deal with processes or character evolution in a variety of taxa rather than a variety of characters in a single higher or lower taxon. Edlinger presents a tantalizing scenario of how torsion may have occurred in gastropods. However, the limited data presented are highly selective. For example, bellerophonts are assumed to have been untorted, a view that is not widely held among malacologists, for example Batten, Rollins, and McLean. Most of the classical works dealing with torsion, such as those by Naef, Garstang, Thompson, and Ghiselin, are not even mentioned. These deficiencies certainly cast doubt on the credibility of the scenario presented here. Voltzow provides us with compelling evidence showing how the pedal musculature of patelloid limpets is fundamentally different from other "limpets," supporting Lindberg's claim that the Patellogastropoda are monophyletic and distinct from other primitive gastropods. Penchaszadeh presents data on the phenomenon of direct development in many species of gastropods from the northern Atlantic coast of South America. Bandel discusses the potential utility of shell microstructure in gastropod phylogeny. Healy provides detailed ultrastructural descriptions of gastropod spermatozoa and suggests that such taxa as *Omalogyra* and the Rissoellidae are allied to the Heterogastropoda and Opisthobranchia, respectively. One major euthyneuran attribute, a glycogen helix, is present in one species of *Rissoella* but absent in another. This suggests several possibilities that could have markedly different interpretations of heterogastropod and euthyneuran phylogeny.

This volume represents a major contribution to our knowledge of gastropod phylogeny. Those who relish traditional classifications and stability in higher molluscan systematics will find little to comfort them. To help ease the pain, Ponder and Warén have provided a detailed appendix outlining Caenogastropoda and Heterostropha classification with all available family group names. Though the contents of this volume provide few definitive conclusions to the problems that have plagued students of gastropod phylogeny and systematics, they certainly represent a major advance in better defining the problems and in suggesting some tentative solutions.

Terrence M. Gosliner

Common and Scientific Names of Aquatic Invertebrates from the United States and Canada: Mollusks. American Fisheries Society Special Publication 16

compiled by D. D. Turgeon, A. E. Bogan, E. V. Coan, W. K. Emerson, W. G. Lyons, W. L. Pratt, C. F. E. Roper, A. Scheltema, F. G. Thompson & J. D. Williams. American Fisheries Society: Bethesda.

This volume represents a prodigious effort by many malacologists in the United States to establish a checklist of scientific and vernacular names for mollusks of the region. The acknowledgments state that 10 authors in addition to the 10 listed on the title page were responsible for compiling the species lists and more than 100 individuals reviewed the species lists.

The geographical coverage includes the Atlantic and Pacific coasts of the United States and Canada, excluding the Hawaiian Islands. This artificial arrangement excludes areas of known biogeographical affinity, such as the coast of Florida with the West Indies and much of the rest of the Caribbean and southern California with much of the Pacific coast of Baja California. This middle ground between political and biogeographical reality is an acknowledged compromise, which unfortunately diminishes some of the utility of the work for those wishing to use it for a resource in the compilation of faunal work.

In addition to the scientific name, including author and date, a geographical designation is provided, as is a common name where it is deemed useful or appropriate. The geographical designation includes notation of the occurrence in the Atlantic, Arctic, or Pacific for marine species, and estuarine, freshwater, or terrestrial designations for other taxa. Established introductions and presumed extinctions are also indicated.

In many cases, there are some problems with the designation of Atlantic and Pacific status. Many tropical taxa, *Lomanotus stauberi* Clark & Goetzfried, 1976 (now known to be a junior synonym of *L. vermiformis* O'Donoghue, 1929), *Aplysia parvula, A. dactylomela,* and *A. juliana* to

name just a few examples, are known from the Atlantic coast of Florida and are designated as Atlantic. However, they are also known from the Pacific coast of Mexico, outside the geographical scope of the work. Their designation as exclusively Atlantic may convey the false impression to the non-specialist that these species are in fact absent from Pacific waters. Others such as *Hermaea vancouverensis* are listed from both the Atlantic and Pacific, but to my knowledge have never been recorded from the Atlantic. If unpublished data are incorporated, it is essential that biogeographers have the source of this information available to them.

Some rather unfortunate systematic errors have crept into the list despite the impressive vigilance of so many reviewers. The Heterodoridae despite their name are arminacean nudibranchs, not dorids. The Spurillidae has been included in the Aeolidiidae by virtually all recent authors. All species of *Coryphella* should be considered as members *Flabellina* in the Flabellinidae rather than Coryphellidae. At least one species, *Acteocina harpa* (Dall, 1871), is correctly listed in the Scaphandridae but again in the Retusidae (as *Colephysis*).

Perhaps the most difficult tasks are to incorporate recently described taxa and taxa placed in synonymy. The list attempts to include all literature prior to 1985, an impossible task. Many taxa described prior to 1985 have simply been overlooked. An even larger number of species have been placed in synonymy, such as *Cuthona stimpsoni* Verrill, 1880, considered as a synonym of *Flabellina salmonacea* (Couthouy, 1839) since Kuzirian's revision of the group in 1979.

The question of the inclusion of common names for species is an issue with which I have some philosophical difficulty. It is unclear as to its necessity, particularly in the case of species that have no commercial value and are not generally known to the lay audience. Creating common names for these species seems to pander to ignorance rather than follow the rationale that all practicing systematists understand. Perhaps more effort ought to be spent educating the public as to the necessity and utility of scientific names and less on dreaming up common names. My four year-old son is not unusual in being able to rattle off *Eucalyptus, Hippopotamus,* or *Tyranosaurus rex.* My own bias notwithstanding, there are problems with some of the common names utilized in the list. Virtually every student of marine biology on the Pacific coast of North America has learned that the common name of *Cryptochiton stelleri* is the gum-boot chiton, not the giant Pacific chiton.

Many common species such as the moon snail *Polinices lewisii* are not given common names, yet we are forced to deal with *Eubranchus misakiensis* as the Misaki balloon aeolis! I particularly resent *Cuthona phoenix,* a species I described, being called the bornagain cuthona. Some of the common names are misleading or erroneous. *Cuthona perca* was originally described from Brazil and has also been recorded from Florida, the Hawaiian Islands, New Zealand, and Lake Merrit in San Francisco Bay. This species

is called the Lake Merrit cuthona, despite the fact that it has been clearly introduced within this estuary. *Chelidonura hirundinina* was called the leech aglaja, erroneously thought to be derived from the leech *Hirudo,* when in fact the name comes from the swallow *Hirundo,* owing to the elongate swallow-like tails of this species. The creation of all these common names requires an index of 119 pages, almost half the volume. Perhaps this space could have been devoted to including known synonyms and more detailed distributional data.

Nevertheless, this book has a great deal of utility. It is a good place to start to know what taxa have been recorded from much of North America, north of Mexico. It is an excellent source of authors and dates, often an essential bit of information that is left out of many checklists. Certainly, it is important for specialists to update the list and provide the most current systematic information available.

Terrence M. Gosliner

Information for Contributors

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Manuscripts must be typed on white paper, 8½″ by 11″, and double-spaced throughout (including references, figure legends, footnotes, and tables). If computer generated copy is to be submitted, margins should be ragged right (*i.e., not* justified). To facilitate the review process, manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics. Metric and Celsius units are to be used.

The sequence of manuscript components should be as follows in most cases: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, figures, footnotes, and tables. The title page should be on a separate sheet and should include the title, author's name, and address. The abstract should describe in the briefest possible way (normally less than 200 words) the scope, main results, and conclusions of the paper.

Literature cited

References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Smith, 1951), for two authors (Smith & Jones, 1952), and for more than two (Smith *et al.,* 1953).

The "literature cited" section must include all (but not additional) references quoted in the text. References should be listed in alphabetical order and typed on sheets separate from the text. Each citation must be complete and in the following form:

a) Periodicals

Cate, J. M. 1962. On the identifications of five Pacific *Mitra.* Veliger 4:132–134.

b) Books

Yonge, C. M. & T. E. Thompson. 1976. Living marine molluscs. Collins: London. 288 pp.

c) Composite works

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117–135. *In:* R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal invertebrates of California. Stanford Univ. Press: Stanford, Calif.

Tables

Tables must be numbered and each typed on a separate sheet. Each table should be headed by a brief legend.

Figures and plates

Figures must be carefully prepared and should be submitted ready for publication. Each should have a short legend, listed on a sheet following the literature cited.

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Upon receipt each manuscript is critically evaluated by at least two referees. Based on these evaluations the editor decides on acceptance or rejection. Acceptable manuscripts are returned to the author for consideration of comments and criticisms, and a finalized manuscript is sent to press. The author will receive from the printer two sets of proofs, which should be corrected carefully for printing errors. At this stage, stylistic changes are no longer appropriate, and changes other than the correction of printing errors will be charged to the author at cost. One set of corrected proofs should be returned to the editor.

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THE VELIGER

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This is meant to make facilities available for publication of original articles from a wide field of endeavor. Papers dealing with anatomical, cytological, distributional, ecological, histological, morphological, physiological, taxonomic, evolutionary, etc., aspects of marine, freshwater, or terrestrial mollusks from any region will be considered. Short articles containing descriptions of new species or lesser taxa will be given preferential treatment in the speed of publication provided that arrangements have been made by the author for depositing the holotype with a recognized public Museum. Museum numbers of the type specimen must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

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Photic Vesicles[1]

by

RICHARD M. EAKIN

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Abstract. A summary is presented of various investigations on unique cytoplasmic organelles—termed photic vesicles—in the eyes of gastropod mollusks. Emphasis is given to the research of the author a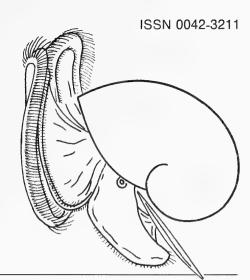nd his associates and to that to Tomiyuki Hara and his colleagues at Osaka University. Some unpublished findings of the Osaka workers are included. The following aspects of the vesicles are covered: structure, origin, fate, and function as transporters of the photopigment retinochrome and calcium. The data are synthesized into a scenario, with a heretofore unpublished diagram, on the cycling of retinochrome in which photic vesicles play a strategic role.

Photic vesicles are remarkable cytoplasmic organelles in the eyes of gastropod mollusks. They are unique in aggregating in very large numbers in the cell bodies of type I photosensory cells (Figures 1, 3), and in carrying a photopigment, hence the term "photic vesicles." They have been studied mostly in pulmonates (*e.g.,* snails and slugs—referenced below), but they occur also in opisthobranchs (*e.g.,* nudibranchs—EAKIN *et al.,* 1967), and in prosobranchs (*e.g.,* periwinkles—MAYES & HERMANS, 1973).

Early History

The vesicles were first observed by two groups of European investigators studying the ultrastructure of the eyes of a snail, *Helix pomatia*: RÖHLICH & TÖRÖK (1963), who described how the vesicles—called *Elementarkörperchen*—form a crystalline mass (*Biokristall*) and SCHWALBACH *et al.* (1963) who regarded the vesicles as a foam (*Schaumstruktur*). The truly vesicular nature of the organelle was confirmed and further described in another snail, *Helix aspersa*, by Mrs. Jean Brandenburger, my research associate for many years, and me (EAKIN & BRANDENBURGER, 1967a).

Recently I learned in a personal communication from Professor Tomiyuki Hara of Osaka University that he and two colleagues, Y. Koshida and A. Tanaka, had studied the eyes of a land snail, *Euhadra callizona amaliae*, in 1963 and observed masses of vesicles in the cell bodies of the photosensory cells. Their findings on the vesicles, however, were not published. I have now received from him an unpublished manuscript with six plates of electron micrographs. It contains much information on the structural and biochemical features of a snail's eye that was regrettably not entered into the scientific literature. The authors had measured the vesicles (40–50 nm in diameter) and had shown the beautiful paracrystalline arrangement of them when compacted.

Dr. Jane Westfall and I had observed the vesicles in *Helix aspersa* in a survey of invertebrate photoreceptors that led to a 1962 symposium paper (EAKIN, 1963), but it was not until 1967 that a description of them was published (EAKIN & BRANDENBURGER, 1967a). In that year we suggested the possibility that the vesicles may carry a photopigment (EAKIN & BRANDENBURGER, 1967b). At the same time a similar function was postulated by HARA *et al.* (1967) in an excellent paper on photopigments in the retina of an octopus. In the discussion they analogized the gastropod vesicles with lamellated bodies in cephalopod photosensory cells shown by them to contain a new pigment termed retinochrome. We gave to the vesicular organelle the name photic vesicle (EAKIN & BRANDENBURGER, 1970).

Structure

The vesicles are spherical when not compressed, and uniform in size (diameter 80–85 nm in *Helix aspersa*). When tightly massed in the perinuclear region of a photosensory cell as normally seen (Figure 1), or when compressed by centrifugation of an eye (REED & EAKIN, 1976), the vesicles become oval and packed into a paracrystalline array. Normally, large granules (35 nm or more) and a few mitochondria are dispersed among the vesicles. All other cytoplasmic structures appear to be shunted aside as the vesicles are produced and accumulated. The granules

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[1] Dedicated to Dr. Rudolph Stohler, Founding Editor of *The Veliger*.

are considered beta particles of glycogen because of their size and digestibility by alpha amylase (EAKIN & BRANDENBURGER, 1967b). These features characterize only type I sensory cells of *H. aspersa*, not type II cells (BRANDENBURGER & EAKIN, 1974; BRANDENBURGER, 1975).

Origin and Fate

We believe that photic vesicles arise in the cell bodies of type I sensory cells by abscission of the ends of the Golgi cisternae—a conclusion based upon electron micrographs (EAKIN & BRANDENBURGER, 1967a) and upon osmium staining (EAKIN & BRANDENBURGER, 1970 see below). KATAOKA (1975), however, ascribes their origin to agranular endoplasmic reticulum (ER) in the slug *Limax flavus* because vesicles were sometimes observed in continuity with the smooth ER and because the vesicles, ER, and the convex side (but not the concave side) of the Golgi apparatus were stained with osmium tetroxide (see symposium discussion in EAKIN & BRANDENBURGER, 1976). In our experience, osmium staining revealed fine granular deposits in the smooth ER, whereas the Golgi apparatus and photic vesicles were intensely blackened. This observation accords with the prevailing dogma on the secretory activity of these organelles. After formation, photic vesicles appear to accumulate in large masses, described above. Then the vesicles move distally within the sensory cells. The movement is probably caused by pulsations of the eye resulting from contractions of unique musculo-secretory cells in the optic capsule (EAKIN & BRANDENBURGER, 1972; MORTENSEN & EAKIN, 1974). The final fate of the vesicles appears from our electron micrographs (EAKIN & BRANDENBURGER, 1982) and from osmium staining (Figure 2, EAKIN & BRANDENBURGER, 1970) to be fusion with smooth ER lying beneath the photoreceptoral microvilli.

Transporters of Photopigment

One of the functions of photic vesicles is transport of photopigment along the pathway just described from perinuclear ER to the microvilli (EAKIN, 1972). Experiments, now presented in approximate chronological order, attest to this function.

Autoradiography: Snails (*Helix aspersa*) injected pericardially with tritiated vitamin A exhibited sequential uptake by Golgi, photic vesicles, and microvilli (EAKIN &

BRANDENBURGER, 1968; BRANDENBURGER & EAKIN, 1970). Although not definitively shown, it was assumed at that time that a snail's eye contains a photopigment whose chromophore is a vitamin A derivative. GILARY & WOLBARSHT (1967) had found by electrical recording that the eye of another snail, *Otala lactea*, exhibited a spectral sensitivity in close agreement with the absorption curve of rhodopsin. Moreover, the Osaka workers, cited earlier, had discovered that green light (525 nm) was absorbed by the microvilli of a land snail (KOSHIDA *et al.*, 1963). Ultimately, OZAKI *et al.* (1986) demonstrated that the vesicles contain the photopigment retinochrome (discussed below). In our papers on the autoradiography of the eye of *H. aspersa*, mentioned above, we postulated that the aggregations of vesicles store a photopigment.
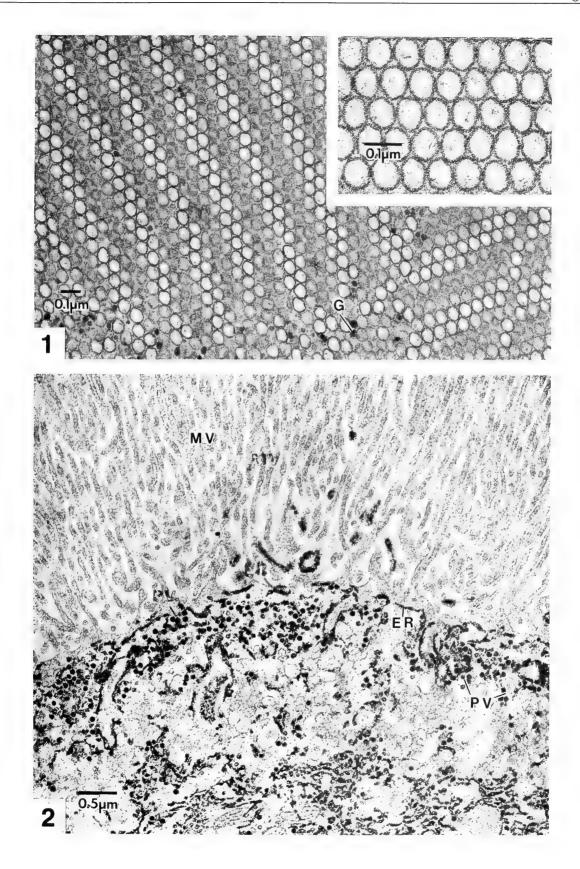
Osmium staining: In contrast to osmium fixation, staining with osmium tetroxide involves impregnation of specimens with the metal by 1–3 days of immersion in unbuffered 2% aqueous solution of OsO_4 at 40° C. When this procedure was applied to the eyes of *Helix aspersa*, the Golgi cisternae and photic vesicles were intensely stained (EAKIN & BRANDENBURGER, 1970). The so-called osmium black is believed to result from OsO_4 reduction by an unsaturated compound such as a vitamin A-containing photopigment. The rod disks of an amphibian (*Xenopus laevis*) were similarly stained. The distal ER beneath the microvilli and the bases of villi in the eyes of *H. aspersa* also showed intense osmiophilia (Figure 2), but distally the villi exhibited only a dusting of osmium black.

Light- and dark-adaptation: The detectable effects of light and darkness on photic vesicles suggest that the vesicles are transporters of photopigment (EAKIN & BRANDENBURGER, 1974). Snails (*Helix aspersa*) kept in total darkness for one to four months exhibited a break-up of the aggregations of vesicles, a marked increase in the production of lysosomes that incorporated the vesicles, and a deposition of multilayered membranous capsules and partitions around and within the masses of vesicles. These features indicated cessation in formation of photic vesicles and a removal of those in storage—a picture not observed in normal (wild) or light-adapted (control) snails. Moreover, in the latter an accumulation of vesicles distally near the microvilli was discernible (EAKIN & BRANDENBURGER, 1967c). The microvilli—the other principal organelles involved in photoreception—also showed ultrastructural changes in response to the presence or absence of light.

→

Explanation of Figures 1 and 2

Figure 1. Electron micrograph of photic vesicles massed near the nucleus of a type I photoreceptoral cell in an eye of the snail *Helix aspersa*. G, glycogen granules. ×50,000. *Inset*: Some photic vesicles at higher magnification. ×100,000. Figure 2. Osmium staining of distal part of a type I photosensory cell in an eye of *Helix aspersa*. Note dense deposits of osmium black in photic vesicles (PV), endoplasmic reticulum (ER), and bases of some microvilli (MV). ×20,000. From EAKIN & BRANDENBURGER, 1970, with permission of *The Journal of Ultrastructure Research*.

Figure 3
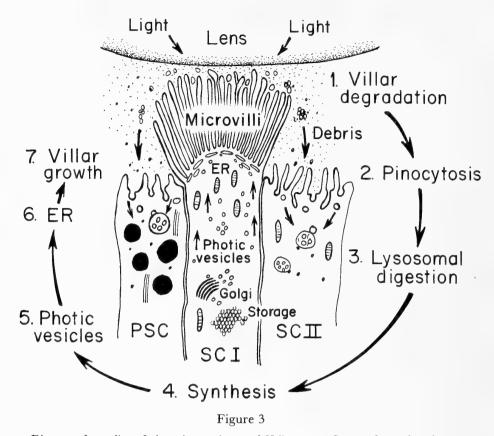
Diagram of recycling of photopigment in eye of *Helix aspersa*. See text for explanation.

In another study, of a light-tolerant slug (*Ariolimax californicus*) and a nocturnal one (*Limax maximus*), we found a difference in the distribution of photic vesicles (EAKIN & BRANDENBURGER, 1975a). In the nocturnal species the vesicles were primarily in the perinuclear regions of the sensory cells, whereas in the diurnal species many vesicles occurred in the distal halves of the photoreceptoral cells, as well as in masses in the cell bodies. All these observations support the hypothesis that light stimulates production, migration, and utilization of photic vesicles.

Autofluorescence: Knowing that vitamin A fluoresces (POPPER, 1944) and that the eyes of *Helix aspersa* contain this vitamin (EAKIN et al., 1974), we examined sections of eyes of that snail by a fluorescence microscope to determine where the vitamin A was situated (EAKIN & BRANDENBURGER, 1978). The microvilli and the masses of photic vesicles immediately fluoresced, emitting a brilliant orange color that faded within 20–30 sec. Sections exposed to white light prior to examination under ultraviolet radiation did not fluoresce. As a control, sections of eyes of an amphibian (*Xenopus laevis*) were similarly treated and studied. The outer segments of the rods and cones fluoresced promptly, but the bright silvery color faded in 20–30 sec. Sections first exposed to white light did not fluoresce. Conclusion:

the photic vesicles may possess a vitamin A-containing compound such as a photopigment. In 1986 OZAKI et al. conducted a fluorescence microscopy study of the eye of a marine conch, *Conomulex luhuanus*, and observed autofluorescence of both microvilli and photic vesicles. There was a difference, however, in the light emitted by the two types of organelles.

Freeze-fracture: Carbon-platinum replicas of the surfaces of fractured, frozen eyes of *Helix aspersa* were studied by electron microscopy (BRANDENBURGER et al., 1976) to obtain information on size and amount of intramembranous particles of photic vesicles and of photosensory microvilli. In light-adapted specimens (versus dark-adapted ones), 70 Å particles on the internal or protoplasmic (P) leaflet of the microvillar membranes were numerous. The particles, in the size range of rhodopsin, were interpreted as photopigment. Most photic vesicles cross-fractured. The vesicular membranes were usually not separated into P and E (external) leaflets, probably because of the small size of the vesicles. In favorable instances, however, in which the vesicular membrane was split, we found very few particles attached to either P or E surfaces. From this investigation I draw the conclusion that the putative photopigment, now known to be retinochrome (see below), is not carried in the vesicular membrane but in solution or colloidal sus-

pension *within* the vesicles. This hypothesis agrees with our earlier demonstration that osmium staining blackened the contents of the vesicles (see Figure 2).

Cell fractionation, biochemistry, microphotometry: My associates and I succeeded in obtaining a cell fraction containing the photic vesicles in *Helix aspersa* (EAKIN *et al.,* 1974). We were unsuccessful, however, in obtaining publishable biochemical and microphotometric data about the contents of the vesicles.

OZAKI *et al.* (1984, 1986) proved the vesicular pigment to be retinochrome by cell fractionation, biochemistry, fluorescence microscopy, and microphotometry in a brilliant multifaceted investigation of the eyes of a marine gastropod, *Conomulex luhuanus.* Moreover, the authors determined that the photopigment in the microvilli is 11-*cis* rhodopsin. Additionally, they found a difference between the photic vesicles in the perinuclear masses and those more distally situated in the pigmented layer of the eye and perhaps also—my conjecture—in the tips of the photosensory cells. The distal vesicles contain only retinochrome, whereas the aggregated vesicles possess retinochrome *and* aporetinochrome. The investigators speculated that the distal vesicles "act as a direct supplier of retinal to the closely located microvilli, whereas the [perinuclear aggregation of vesicles] serves as a storage place for retinal in retinochrome and for newly formed aporetinochrome."

Similar results in the marine snail *Bulla gouldiana* were reported recently in an abstract of a poster by BOGART *et al.* (1989). Using the fluorescence technique of OZAKI *et al.* (1986) Bogart and her colleagues observed that the "distal segments" of the photoreceptors contained rhodopsin whereas retinochrome was found in the "soma layer" of the receptoral cells. Although photic vesicles were not mentioned, presumably masses of them are situated in the somatic regions of the photosensory cells of *Bulla,* as in other snails.

Bearers of Calcium

Because calcium is an important catalyst in many physiologic processes including photoreception, we investigated the possibility that photic vesicles transport this element in addition to photopigment. Using a non-dispersive X-ray analyzer we showed that the nuclear layer of a *Helix aspersa* eye, wherein lie the masses of vesicles, contains a high concentration of calcium (EAKIN & BRANDENBURGER, 1975b). This finding does not, of course, prove that calcium is in the vesicles. Then we (EAKIN & BRANDENBURGER, 1980) fixed eyes of *H. aspersa* in glutaraldehyde and treated them with potassium pyroantimonate. Electron microscopy of unstained ultrathin sections of the eyes revealed a dense granule in the center of each photic vesicle. The granules were interpreted as precipitated calcium complexed with pyroantimonate. Credence to this conclusion was provided by the results of experiments in which sections of the same eyes were floated on a solution of the chelating agent EGTA before examining them in an elec-

tron microscope. The granules were absent! Conclusion: photic vesicles contain calcium.

A Scenario

In Figure 3 (heretofore unpublished) I summarize the supposed major events in a gastropod eye in which photic vesicles play an important role.

Villar degradation: Light, after passing through the cornea and lens of a snail's eye, strikes the photoreceptoral microvilli. The photoresponse causes the breakdown of the microvillar membranes, especially at the tips (EAKIN & BRANDENBURGER, 1982).

Pinocytosis: The debris from the above event is taken up by pinocytosis and phagocytosis by retinal cells, especially type II sensory cells and pigmented supportive cells (EAKIN & BRANDENBURGER, 1982; BRANDENBURGER & EAKIN, 1983).

Lysosomal digestion: The internalized pinocytic and phagocytic vesicles fuse with primary lysosomes, which contain digestive enzymes (*e.g.,* acid phosphatase), to form secondary lysosomes (EAKIN & BRANDENBURGER, 1974; BRANDENBURGER, 1977; BRANDENBURGER & EAKIN, 1983).

Synthesis: The products of lysosomal digestion reach the synthetic centers—ER and Golgi apparatus—of type I sensory cells where the recycled molecules become incorporated into aporetinochrome and retinochrome and packaged into photic vesicles.

Photic vesicles: Photic vesicles released from the ER and Golgi cisternae (accelerated by light) are stored in large masses near the nuclei of type I sensory cells. The vesicles are moved distally, supposedly by pulsations of unique cells in the optic capsule that contain smooth muscle fibers (EAKIN & BRANDENBURGER, 1972). This process is also accelerated by light.

Smooth endoplasmic reticulum: Upon reaching the distal ends of the sensory cells, the photic vesicles fuse with smooth cisternae beneath the microvilli, releasing retinochrome and other vesicular contents (EAKIN & BRANDENBURGER, 1982).

Villar growth: I speculate that the microvilli are regenerated by basal addition of membrane constituents. Molecules of photopigment and perhaps other compounds become incorporated into the microvillar membranes, now ready for light reception again.

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ology, especially its artist, Phyllis Thompson Spowart, who prepared Figure 3. Integrative Biology is a successor of the Department of Zoology, my academic home for 60 years (1929–1989).

Added in proof: A. W. CLARK (1963, Jour. Cell. Biol. 19:14A) reported many "550 Å spheres" in retinular cells of a snail (*Viviparus maleatus*).

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Continuous Reproduction and Episodic Recruitment of *Lacuna vincta* (Montagu, 1803) in the Gulf of Maine

by

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Abstract. Studies of *Lacuna vincta* (Montagu, 1803) limited to the intertidal zone suggest a seasonally defined spawning period. This study, conducted in the subtidal zone, reports continuous spawning year round from Cape Ann, Massachusetts, to Mt. Desert Island, Maine. Larval recruitment occurred in four pulses during an intensive two-year study in Magnolia, Massachusetts. Shell-height frequency distributions of *L. vincta* were bimodal for most months sampled, indicating that overlapping cohorts existed in the population.

INTRODUCTION

Lacuna vincta is a small gastropod with demersal eggs and planktonic larvae that inhabits the rocky littoral and sublittoral zones of the North Atlantic (NORTON, 1971; SMITH, 1973; FRALICK *et al.*, 1974; RUSSELL-HUNTER & MCMAHON, 1975; FRETTER & MANLY, 1977; GRAHAME, 1977; SHATLOCK & CROFT, 1981; SOUTHGATE, 1982; THOMAS & PAGE, 1983; WITMAN, 1985; MANEY, 1986). Adults feed on various species of algae (especially kelps) and lay their eggs in a clear gelatinous ring-shaped capsule on the food plant (SMITH, 1973).

Numerous studies report a single, well-defined spawning period for *Lacuna vincta*, but disagree as to its timing and duration (January–June, SMITH, 1973; January–March, SOUTHGATE, 1982; January–October, RASMUSSEN, 1973; March–June, RUSSELL-HUNTER & MCMAHON, 1975; June–August, THOMAS & PAGE, 1983). SOUTHGATE (1982) suggested that the spawning period may be directly related to latitude. Both SMITH (1973) and SOUTHGATE (1982) derive life-history parameters for populations of *L. vincta* based on the assumption of one cohort per year produced in a single, restricted spawning period.

An intensive long-term study of *Lacuna vincta* in Massachusetts shows that continuous reproduction is occurring in subtidal populations, and observations along the coast of Maine indicate that the habit of continuous spawning extends into higher latitudes. During a two-year period four distinct cohorts existed in Magnolia and overlapped in time. Life-history tables of *L. vincta* based on the assumption of a single cohort derived from a restricted breeding period must be reevaluated in light of the possibility that the underlying data involved overlapping cohorts.

MATERIALS AND METHODS

Forty-eight SCUBA dives were conducted in Popplestone Cove, Magnolia, Massachusetts, from July 1982 to October 1984. During each of these dives, kelp blades were observed for the presence or absence of egg masses. In addition, six randomly selected whole kelp plants (3 each of *Laminaria saccharina* and *L. digitata*) were collected monthly (5 months were missed owing to inclement weather), placed into 0.5-mm mesh nytex bags, and tied off with Velcro straps. This technique sampled all the snails in 0.2 m^2 of the kelp bed population of *Lacuna vincta* because all the snails in the kelp bed were on kelp fronds. In the lab, each sample was fixed in 10% formalin. The snails were counted and separated from the kelp.

Approximately 100 snails from each monthly sample were measured to the nearest 0.1 mm from the tip of the shell apex to the lowest point of the aperture, using an ocular micrometer in a binocular microscope at ×10 magnification. Individuals from each month were placed into shell-height categories of 0.5 mm, and the frequency distributions were plotted as histograms. Using the method of CASSIE (1954) and HARDING (1947) these height measurements were also plotted on probability paper, and the inflection points in the resulting lines were used to distinguish coexisting size classes. For each size class on each sampling date, mean shell height was determined by replotting on probability paper. These mean shell heights were then plotted over time to show more clearly the cohorts of *Lacuna vincta* observed in Popplestone Cove during the 28 months of regular sampling.

During 1985 and 1986, 20 dives were made in Popplestone Cove throughout the year to observe the presence or
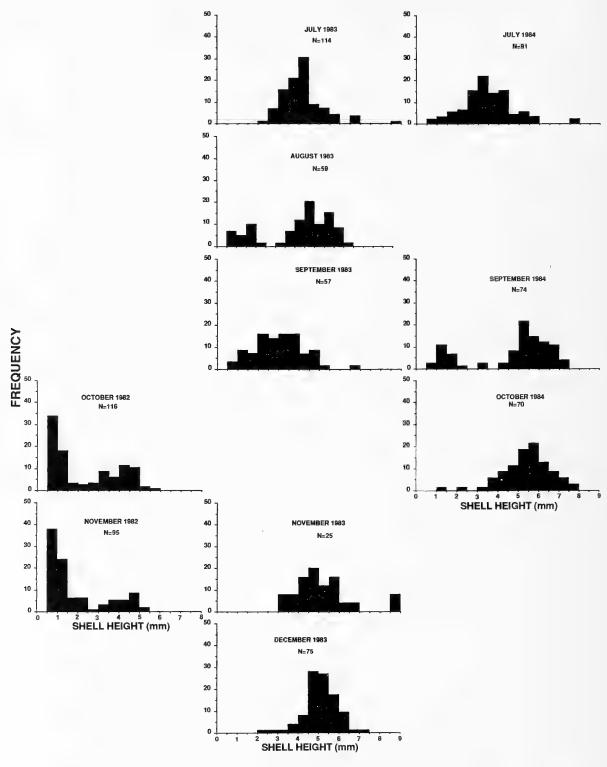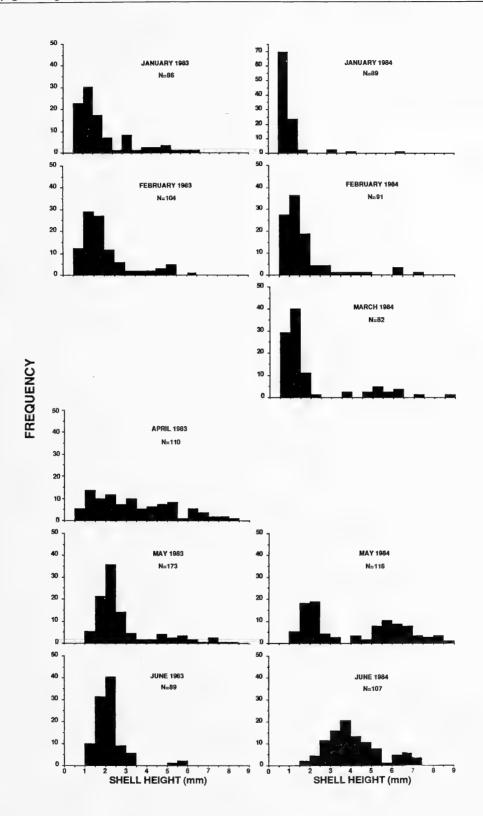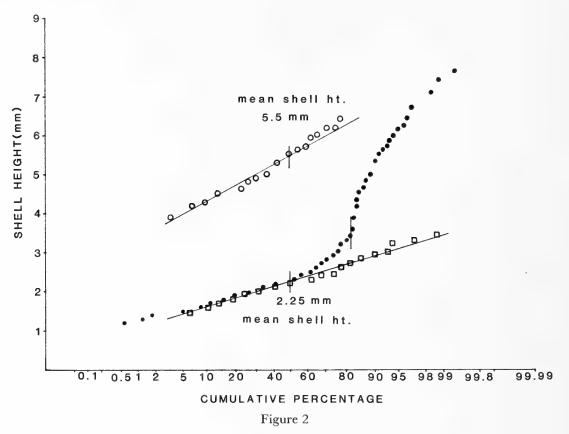
Figure 1

Shell-height frequencies for *Lacuna vincta* in Magnolia, Massachusetts, for October 1982 to October 1984. This figure spans two pages. To follow the temporal sequence, start with October 1982 in the first column, proceed below to November 1982, and then go to January 1983 on the facing page.

Figure 2

A probability plot of the shell-height data for May 1983. Closed circles depict the entire sample, with a vertical line indicating the inflection point. The two lines drawn with open symbols represent the two data sets on either side of the inflection point, each renormalized to a total of 1.00 to depict two size cohorts.

absence of *Lacuna vincta* egg masses. Trips were made in October, November, and December 1986 to Ogunquit and Mt. Desert Island, Maine, to determine whether *L. vincta* was laying eggs in more northerly latitudes at those times.

RESULTS

We observed *Lacuna vincta* egg masses on blades of the kelps *Laminaria saccharina* and *L. digitata* in Popplestone Cove on all 68 dives throughout the four-year duration of this study (July 1982 to September 1986), indicating that reproduction is continuous at this site.

Shell height of *Lacuna vincta* in Popplestone Cove varied from a minimum of 0.5 mm to a maximum of 13 mm. Frequency distributions of the shell height of *L. vincta* show clear bimodal distributions in some months and possible bimodal distributions in others (Figure 1). To determine whether more than one size class was present at any given time, the cumulative shell-height frequency was plotted on arithmetic probability paper (*e.g.*, Figure 2). A straight line indicates that shell-height frequencies are normally distributed, whereas a sigmoidal curve indicates a bimodal distribution of shell-height frequencies (HARDING, 1947; CASSIE, 1954). Two normally distributed size

classes can be distinguished by considering the portions of the line above and below the inflection points as independent classes. Of 20 samples collected from October 1982 to October 1984, two samples contained a single size class, and 18 samples contained two size classes (Table 1). This suggests that recruitment, unlike reproduction, is *not* continuous for this population. Replotting the portions as lines with 100% cumulative frequency yields for each class the mean shell height, which corresponds to the shell height at the 50% cumulative percentage for the respective replotted lines.

As can be seen by comparing the May 1983 histogram (Figure 1) to the May 1983 probability plot (Figure 2), size classes are more easily distinguished by the inflection points than by inspection of the histograms, but it must be remembered that the probability plot technique is also an "eyeball" method. Misjudgement of an inflection point due to visual error or sampling error may result in the miscalculation of the mean shell height for a size class. It is relatively easy to follow particular size classes over time, especially for *Lacuna vincta* in Popplestone Cove, which typically had two well-separated size classes in each monthly sample.

Five such size classes can be distinguished in a plot of

Table 1

Sample size (*n*) for monthly samples of *Lacuna vincta* in Popplestone Cove, Magnolia, Massachusetts, and mean shell heights for size classes detected by plots on probability paper. For clarity, mean shell heights are arranged among six arbitrary categories: XSM (0–1.50 mm), SM (1.55–2.00 mm), MED (2.05–3.50 mm), L (3.55–5.00 mm), XL (5.05–5.95 mm), XXL (≥6.00 mm). The solid lines group together size classes that are plotted as presumed cohorts in Figure 3.
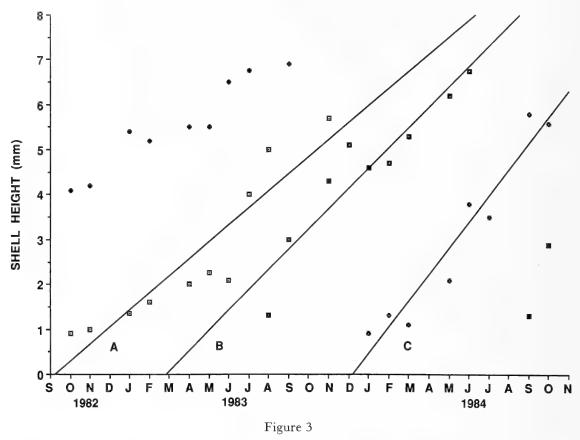
Month	n	XSM	SM	MED	L	XL	XXL
Oct-82	116	0.9 (58%)			4.1 (42%)		
Nov-82	95	1.0 (72%)			4.2 (28%)		
Dec-82	—						
Jan-83	86	1.35 (80%)				5.4 (20%)	
Feb-83	104		1.6 (86%)			5.2 (14%)	
Mar-83	—						
Apr-83	110		2.0 (61%)			5.5 (39%)	
May-83	173			2.25 (81%)		5.5 (19%)	
Jun-83	89			2.1 (94%)			6.5 (6%)
Jul-83	114				4.0 (80%)		6.75 (20%)
Aug-83	59	1.3 (24%)			5.0 (76%)		
Sep-83	57			3.0 (98%)			6.9 (2%)
Oct-83	—						
Nov-83	25				4.3 (58%)	5.7 (42%)	
Dec-83	75					5.1 (100%)	
Jan-84	89	0.9 (96%)			4.6 (4%)		
Feb-84	91	1.3 (90%)			4.7 (10%)		
Mar-84	82	1.4 (82%)				5.3 (18%)	
Apr-84	—						
May-84	116			2.1 (50%)			6.2 (50%)
Jun-84	107			3.8 (85%)			6.75 (15%)
Jul-84	91			3.5 (100%)			
Aug-84	—						
Sep-84	74	1.3 (24%)				5.8 (76%)	
Oct-84	70		2.9 (8%)				6.0 (92%)
Total	1823						

mean shell height over time for our samples of *Lacuna vincta* in Popplestone Cove (Figure 3). Two of these size classes appear to be represented in their entirety, and a third, followed over a period of 10 months, showed almost the full range of shell height. The potential for inaccuracies in the determination of monthly mean shell heights precludes the use of this technique to certain quantitative life-history features such as growth curves, but additional analysis may further test the evidence that recruitment in this population is episodic rather than continuous. Linear regression and ANCOVA analysis (SOKOL & ROHLF, 1981) were applied to these three size classes to determine whether they should be considered as real cohorts (in this case, sets of individuals that recruited at the same time), which would have distinct origins in time but similar average growth rates. The three regression equations are provided below.

Class A: Shell Height = 0.3801(Time) − 0.1084
Class B: Shell Height = 0.4527(Time) − 2.6601
Class C: Shell Height = 0.5856(Time) − 8.9195

ANCOVA confirms the impression gained from inspection of these equations and Figure 3: the three size classes have distinctively different origins in time as shown by the significant differences in y-intercepts ($P \ll 0.01$); but they are indistinguishable with respect to average growth rate, since the slopes of the three lines are not significantly different ($P = 0.33$).

To determine whether egg laying was occurring year round at more northern latitudes, trips were made to Maine in October, November, and December 1986. On 29 October 1986, *Lacuna vincta* eggs were observed on the blades of the kelp *Laminaria digitata* that had washed up on Little Hunters Beach in Acadia National Park. *Lacuna vincta*

Figure 3

Average shell height versus time for size classes of *Lacuna vincta* in Magnolia, Massachusetts. The points are clustered into classes of a single presumed cohort; solid lines indicate average growth rates for these cohorts as determined by linear regression.

egg masses, juveniles, and adults were also observed on *Laminaria saccharina* blades washed up on the beach at Seal Harbor, Mt. Desert Island, Maine. On 2 November 1986, *Lacuna vincta* adults, juveniles, and egg masses were observed on *Chondrus crispus* at Perkins Cove in Ogunquit, Maine. *Lacuna vincta* egg masses were again observed at Ogunquit and Mt. Desert Island on 2 and 3 December 1986.

DISCUSSION

Our data show that spawning in *Lacuna vincta* is continuous, with year-round reproduction over a latitudinal range (42°30′ in Magnolia, Massachusetts, to 44°30′ in Mt. Desert Island, Maine) which is farther south than the sites in England and Ireland studied by SMITH (1973) and SOUTHGATE (1982). This finding is consistent with the observation of FRETTER & SHALE (1973) that *L. vincta* larvae are present in the water column off the coast of Plymouth, England, throughout the year, with veligers taken in hauls during every month of the year except three (February, June, and July).

These findings conflict with the suggestion of SOUTHGATE

(1982) that duration of a restricted spawning period may be directly related to latitude in *Lacuna vincta*. Regional differences in environmental features such as climate could possibly account for the difference between our findings on reproductive activity in North America and the findings of SMITH (1973) and SOUTHGATE (1982) in Great Britain. On the other hand, the assumption of SMITH (1973) and SOUTHGATE (1982) that *L. vincta* has a single annual spawning period may derive from the fact that they both restricted their studies to the littoral zone. THOMAS & PAGE (1983) report a sudden appearance of *L. vincta* in the littoral zone of New Brunswick, Canada, in June, and suggest that migration may occur from the sublittoral zone to the littoral zone at this time. SMITH (1973) reports similar findings in England, and during the winter months we have found adult *L. vincta* in sublittoral habitats when they were absent from littoral habitats. Studies of the life history of *L. vincta* should include the subtidal part of the population.

If intertidal subpopulations of *Lacuna vincta* in England experience immigrations from subtidal populations and/or more than one cohort per year, as observed in North America, then the life-history information provided by

SMITH (1973) and SOUTHGATE (1982) may be inaccurate. Both studies calculate mortality based on the assumption of a closed intertidal population comprised of a single cohort in each year.

Regression and ANCOVA indicate that the two distinct size classes observed for 18 of 20 monthly samples of the *Lacuna vincta* population at Magnolia are representatives of different sets of individuals that recruited at the same time (which we refer to as cohorts). Regressed against time, monthly mean shell heights ascend through the same range of values, as would be expected if size classes are actually cohorts growing over time. ANCOVA shows that the size classes followed through time all grow at the same rate, as would be expected for different cohorts of a given population. Four of the five cohorts seen were initiated during our study, one each for the months of August, September, October, and January. Because egg masses were observed year round, this indicates that reproduction was occurring in Magnolia throughout the year, but that recruitment occurred in pulses.

The causes of variable recruitment of marine invertebrates are still poorly known, but two components are believed to be involved: (1) variation in reproductive output and (2) variation in mortality and distribution of larvae while in the water column (GAINES & ROUGHGARDEN, 1987). In Popplestone Cove, the occurrence of five distinct cohorts over 25 months of continuous reproduction indicates pulsed recruitment to this subtidal *Lacuna vincta* population similar to the pulsed recruitment seen to limit density in some intertidal populations (PAINE, 1977; SUTHERLAND & ORTEGA, 1986; GAINES & ROUGHGARDEN, 1987). Because *L. vincta* has continuous reproductive output, the pulsed recruitment observed in this subtidal population is likely to be the result of temporal variation of either events of transport into Popplestone Cove or larval mortality. Further field work on organisms like *L. vincta* is needed to identify the environmental factors that produce pulsed recruitment in subtidal populations, and to determine the importance of these factors to population regulation.

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Recruitment of the Estuarine Soft-Bottom Bivalve *Polymesoda caroliniana* and Its Influence on the Vertical Distribution of Adults

by

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Abstract. In the Sopchoppy-Ochlockonee estuary of northern Florida, adults of the infaunal corbiculacean bivalve *Polymesoda caroliniana* occur in the intertidal zone and, rarely, subtidally. Examinations of the distribution of juveniles and the pattern of recruitment into defaunated sediments indicate that vertical zonation in *P. caroliniana* is determined either at settlement or very shortly after settlement. Reciprocal transplants of subtidal and intertidal sediments, as well as manipulations of presence or absence of adult *P. caroliniana* suggest that *P. caroliniana* larvae settled selectively at intertidal elevations and actively selected an intertidal substratum.
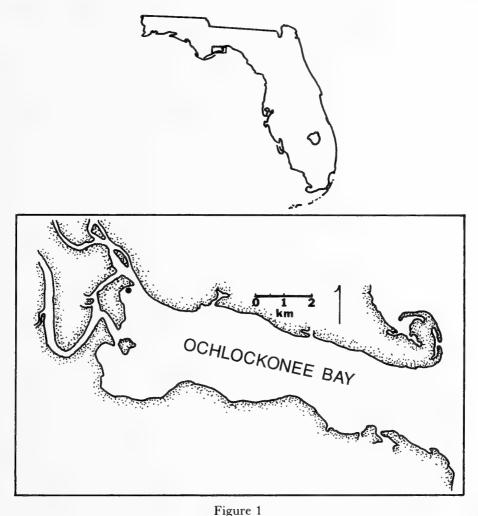
INTRODUCTION

Vertical zonation of benthic organisms is an easily observed phenomenon in marine intertidal areas that has been explained as resulting from interactions of physical and biological factors with the dispersal patterns and survival rates of benthic organisms (see reviews by DAYTON, 1984; UNDERWOOD & DENLEY, 1984). Although CONNELL (1972) generalized that physical factors control upper distributional limits and biological factors control lower bounds, zonation is a complex and often site-specific event that is not easily interpreted (UNDERWOOD & DENLEY, 1984; ROUGHGARDEN et al., 1988). There have been numerous studies of vertical zonation and boundary phenomena on rocky shores (e.g., CONNELL, 1961a, b, 1972; FRANK, 1965; PAINE, 1966, 1974; DAYTON, 1971; MENGE, 1976), but similar studies concerning soft-bottom intertidal areas are comparatively uncommon (WOODIN, 1974, 1976; VIRNSTEIN, 1977; PETERSON & ANDRE, 1980; DAYTON, 1984), primarily because of the inherent difficulties in censusing and experimentally manipulating the generally small or mobile infauna (DAYTON & OLIVER, 1980). Most of the research on soft-bottom intertidal macro-invertebrates has basically concurred with the classic notion of CONNELL (1972) that physical factors limit upper bounds and biological factors control lower bounds (DEXTER, 1969; GREEN & HOBSON, 1970; HOLLAND & POLGAR, 1976; HOLLAND & DEAN, 1977). However, GREEN (1968) suggested that a lack of adequate feeding time can preclude organisms from intertidal regions, and WOODIN (1974) demonstrated that both biological and physical factors were involved in the control of some intertidal polychaete distributions, but added that physical factors should be more important intertidally. Because of the paucity of rigorous manipulative studies and the general lack of data, it is unclear how the principles of intertidal zonation, developed from studies of rocky intertidal habitats, apply to soft-bottom habitats.

A current focus of research is the role of larvae in determining the vertical zonation of marine benthic invertebrates. In order to assess the effects of physical and biological factors on vertical distribution, the significance of larval dispersal in the nearshore environment and settlement in the intertidal habitat must be understood (CONNELL, 1985; ROUGHGARDEN et al., 1988). Unfortunately the planktonic phase remains unknown for the vast majority of species (CONNELL, 1985). In the absence of data on settlement, information on recruitment (*sensu* BUTLER & KEOUGH, 1981; KEOUGH & DOWNES, 1982) can be useful, if carefully interpreted (but see cautions by HADFIELD, 1986; WOODIN, 1986). Available data indicate that many larvae settle non-randomly (MEADOWS & CAMPBELL, 1972; CRISP, 1974; STRATHMANN et al., 1981; GROSBERG, 1982; HANNAN, 1984; BUTMAN et al., 1988), and that the vertical range of adults may be further narrowed (CONNELL, 1961a, b; DAYTON, 1971; STRATHMANN & BRANSCOMB, 1979) suggesting that both settlement and

Figure 1

Map of Florida. Inset shows Ochlockonee Bay (29°58′N, 84°25′W); ● indicates location of study site.

post-settlement events are important. It is unclear for most species whether active habitat selection, passive deposition, or a combination of passive and active modes are involved (BUTMAN, 1987).

In this paper, I document the vertical distributions of adults and recruits of the corbiculacean bivalve *Polymesoda caroliniana* (Bosc, 1801) in a north Florida estuary, document that the vertical distribution of adults is identical to that of recruits, and discuss ways in which this pattern may arise.
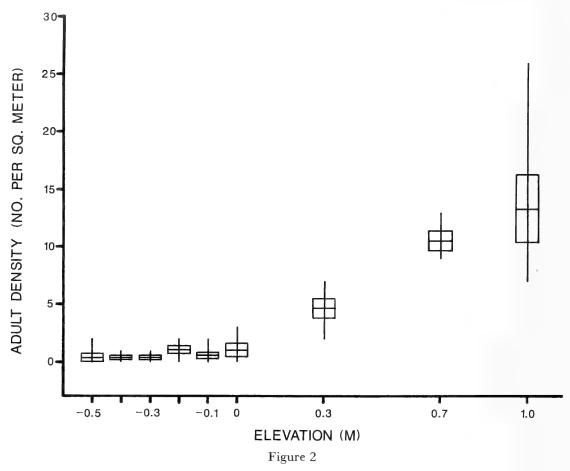
MATERIALS AND METHODS

Study Site

Surveys and experiments were performed in the oligohaline portion of the Sopchoppy-Ochlockonee estuary of northern Florida (Figure 1). This shallow, turbid, and well-mixed estuary is typical of many estuaries fringing the Gulf of Mexico. The estuary is bordered by an exten-

sive stand of *Juncus roemerianus* between the elevations 0 and +1.0 m. Elevations for the study area, determined by surveying tidal levels in relationship to a USCGS benchmark, are reported as deviations from MLLW (mean lower low water). The tidal range in the vicinity of the study site is approximately 1.2 m (OLSEN, 1973).

Adult Distribution

Preliminary surveys indicated that hand-collected samples were necessary to accurately assess adult (clams greater than 20 mm in length [OLSEN, 1976]) distributions. A rectangular 18 × 27 m plot was delineated in the field. The shoreward edge of this rectangle was a line, parallel to the shoreline, located at an elevation of +1.0 m. The seaward edge of the rectangle was located at an elevation of −0.5 m. This rectangle was subdivided into six laterally placed blocks, with nine vertical strata in each block. Vertical strata are defined as areas of bottom at different

Figure 2

Abundance of adult *Polymesoda caroliniana* by elevation at the study site in Ochlockonee Bay. Data from all sampling dates are included. Figures display range, mean, and ±1SE.

elevations. Beginning in September 1982, one block from each stratum was selected randomly for sampling. Samples were collected every two months for one year and no block was sampled more than once. Because adult and juvenile surveys were designed for randomized block analysis, only one observation per cell was taken. This is not an unintentional lack of replication, and in any case the survey data are presented in this paper simply to demonstrate the pattern of vertical distribution shown by adult and juvenile stages. All clams were removed from a 1-m² quadrat placed randomly within the 3 × 3 m stratum-by-block sampling cells selected for a particular sampling date. Clams removed from these quadrats were labeled according to collection location, counted, and preserved, and their linear dimensions were measured. At the conclusion of the sampling period, all 54 stratum-by-block combinations had been sampled.
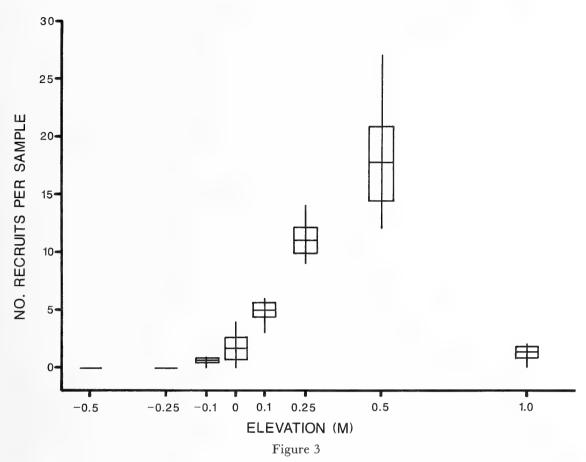
Juvenile Distribution

Because the adult survey disturbed large areas of the bottom, I sampled for recruits and small juveniles (clams

Table 1

Polymesoda caroliniana. Abundance and distribution of juveniles from upper Ochlockonee Bay study site, 1982–1983. Numbers at each elevation and date are numbers per m².

Eleva-tion (m)	Date					
	Sep-82	Nov-82	Jan-83	Mar-83	May-83	Jul-83
+1.0	230.8	57.7	365.4	500.0	307.7	557.7
+0.7	653.8	1942.3	1230.7	173.1	2403.8	519.2
+0.3	76.9	19.2	19.2	38.5	38.5	38.5
0	57.7	0	0	19.2	0	19.2
−0.1	0	19.2	0	0	0	0
−0.2	19.2	0	0	0	0	0
−0.3	0	0	0	0	0	0
−0.4	0	0	0	0	0	0
−0.5	0	19.2	0	0	0	0

Figure 3

Abundance of *Polymesoda caroliniana* recruits to defaunated cores along a vertical gradient in upper Ochlockonee Bay, September to October 1982. Figures display range, mean, and ±1SE.

less than 1 yr old and less than 20 mm in length) of *Polymesoda caroliniana* in an adjacent plot. The juvenile survey area was identical in dimension and elevation to the adult survey area. Again, there were 54 stratum-by-block combinations. Each of the nine vertical strata was sampled every two months, and only one block per stratum was sampled on each date. No block-by-stratum combination was sampled more than once. Beginning in September 1982, one randomly located grab sample was taken from each of the nine randomly selected sample cells for that sample date. Samples were collected using a modified large Ekman grab (WILDCO® 197-G10, area of bite 0.052 m²) and were washed on a 500-μm sieve. Materials retained were preserved, and bivalves were subsequently sorted and counted.
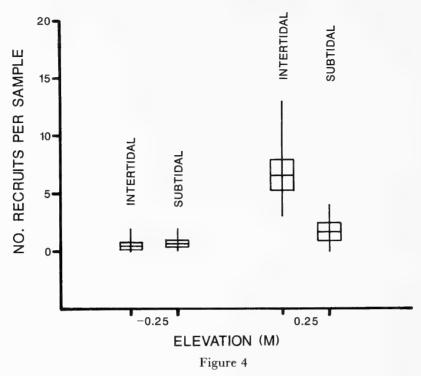
Distribution of Recruits

An additional transect extending between the elevations +1.0 to −0.5 m, and perpendicular to the shoreline, was established near the survey site in September 1982. Cores of surface area 0.014 m², and 1 L in volume, were taken in triplicate at the following elevations: +1.0 m, +0.5 m,

+0.25 m, +0.1 m, 0.0 m, −0.1 m, −0.25 m, and −0.5 m. These elevations were roughly equivalent to the elevations of the strata used in the adult and juvenile surveys. Cores were placed in 1-L polypropylene beakers, defaunated by freezing, and returned to the experimental site at the same elevations from which they were removed. After 1 month, the cores were retrieved and all *Polymesoda caroliniana* recruits counted. This experiment was performed in September because this was a time of heavy settlement (pers. obs.).

Recruit Selectivity

To determine if larvae were settling selectively based on elevation or origin of substrate, an experiment was conducted in December 1982 (when, once again I observed settlement to be dense). Twelve cores (surface area 0.014 m², volume 1 L) were collected from the study site at each of two tidal elevations, +0.25 m and −0.25 m, and defaunated by freezing. Twelve adult *Polymesoda caroliniana* were collected and one adult was placed in each of six intertidal cores and six from the subtidal elevation. Three replicates of each of the following combinations were placed

Figure 4

Recruitment of *Polymesoda caroliniana* to defaunated cores at tidal elevations +0.25 m and −0.25 m, December 1982 to January 1983. Each elevation had replicates of sediment of both intertidal and subtidal origin. Figures display range, mean, and ±1 SE.

at the elevations +0.25 and −0.25 m: intertidal sediments alone, intertidal sediments with one adult *P. caroliniana*, subtidal sediments alone, and subtidal sediments with one *P. caroliniana*. The sediment level in each core was flush with the surrounding substratum. After 1 month the cores were retrieved, and all *P. caroliniana* recruits were counted.

Voucher Specimens

Specimens of *Polymesoda caroliniana* collected in the course of this research have been deposited in the Florida Department of Natural Resources Invertebrate Collection, lot number FSBCI 37174.

RESULTS

Adult Distribution

Across all sampling dates nearly 90% of adult *Polymesoda caroliniana* collected were found to occur intertidally (Figure 2). The greatest abundance was in the highest stratum, +1.0 m, and only occasionally were adults collected subtidally.

Juvenile Distribution

Juvenile *Polymesoda caroliniana* were collected almost exclusively from intertidal elevations (Table 1). Ninety-eight percent of the juveniles collected in the course of this

study occurred at intertidal elevations, with the greatest concentration at the +0.7 m elevation. Juveniles were rare below MLLW.

Distribution of Recruits

Ninety-four percent of the *Polymesoda caroliniana* recruitment into defaunated sediments occurred at intertidal elevations, with the greatest concentration at +0.5 m (Figure 3). Recruitment to subtidal elevations was extremely rare. These data indicate that recruitment occurs across a vertical range nearly identical to that of the juvenile and adult stages.

Recruit Selectivity

Polymesoda caroliniana recruited predominately to intertidal elevations (87% of all recruits; Figure 4), confirming results of the previous recruitment experiment. The data suggest that *P. caroliniana* recruits more heavily to intertidal sediment in preference to subtidal sediment when both are located at the same elevation. The results further suggest that larvae will not settle in the subtidal, even into sediment of intertidal origin. Recruitment data were analyzed utilizing a two-way completely randomized ANOVA. Although there were 24 experimental chambers, data from the subtidal chambers were eliminated; virtually no recruitment occurred subtidally, and the large number of

Table 2

Analysis of variance for effects of sediment type and presence or absence of
conspecific adults on recruitment of *Polymesoda caroliniana*.

Source	d.f.	SS	MS	*F*	*P*-value
Sediment type	1	70.08	70.08	7.19	$0.05 > P > 0.025$
Adult presence/absence	1	0.75	0.75	0.077	$P > 0.25$
Sediment type by adult presence/absence	1	0.08	0.08	0.008	$P > 0.25$
Residual	8	78.00	9.75		
Total	11	148.92			

zeroes violates the assumption of normality of residuals underlying the *F*-test. Sediment type had a strong effect on the recruitment of *P. caroliniana* juveniles ($0.025 < P < 0.05$), but the presence of adult *P. caroliniana* had no detectable effect (Table 2).

DISCUSSION

The present experiments indicate that *Polymesoda caroliniana* recruited primarily to the intertidal and shallow subtidal areas of the study site, a pattern that is reflected in the vertical distributional pattern of juvenile and adult *P. caroliniana*. The concordant patterns of recruit, juvenile, and adult vertical distributions imply that larval settlement preferences play a key role in casting the distributions of post-settlement stages. This conclusion is further supported by the results of the substratum transplant experiments. Nevertheless, because larval settlement was not directly observed it remains possible that elevation-specific differences in early post-settlement mortality play some role in casting the distributions of post-settlement individuals. *Polymesoda caroliniana* larvae could settle preferentially in the vertical range occupied by adult clams. Larvae may be induced to settle in response to cues from specific substrata, microbial faunas, conspecifics, or specific flora (KNIGHT-JONES, 1953; WILLIAMS, 1964; BAYNE, 1969; KNIGHT-JONES *et al.*, 1971; MEADOWS & CAMPBELL, 1972; CRISP, 1974; KECK *et al.*, 1974; CAMERON & SCHROETER, 1980; STRATHMANN *et al.*, 1981; HIGHSMITH, 1982; HUI & MOYSE, 1982; SCHMIDT, 1982). Larvae may also recruit passively through active selection of vertical position in onshore moving water masses (FORWARD, 1976; GROSBERG, 1982; GAINES *et al.*, 1985). Finally, larvae may act as passive particles during settlement, being deposited on the substratum at sites where particles with fall velocities similar to larvae initially settle (HANNAN, 1984; BUTMAN, 1987; BUTMAN *et al.* 1988). It is not known, however, what mechanisms are involved in the pre-settlement distribution and actual settlement of *P. caroliniana* larvae.

Results of the present research suggest that *Polymesoda caroliniana* larvae, when offered a choice in the field, settle preferentially on intertidal sediments rather than subtidal sediments. However, *P. caroliniana* larvae were not induced into settling subtidally into intertidal sediment plots as

STRATHMANN *et al.* (1981) were able to induce *Balanus glandula* to settle on sub-optimal lower substrata. Settlement and recruitment patterns can be quite different because of post-settlement effects (CAFFEY, 1985; CONNELL, 1985; KEOUGH & DOWNES, 1986), but because I observed virtually no subtidal recruitment, settlement is probably rare subtidally unless mortality is rapid and high compared to that at intertidal levels. Results of my work suggest that recruitment reflects settlement in the *P. caroliniana* population that I studied, and by inference that settlement is probably the determining factor in the vertical distribution of adults.

ACKNOWLEDGMENTS

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Additional Opisthobranch Mollusks from Oregon, with a Review of Deep-Water Records and Observations on the Fauna of the South Coast

by

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Abstract.   New and previously overlooked records add 16 species to the list of benthic opisthobranchs known from Oregon, bringing to 83 the total known. The ranges of *Acanthodoris rhodoceras*, *Cuthona lagunae*, *Pleurobranchaea californica*, and *Tenellia adspersa* are extended northward, and those of *Colga pacifica* and *Dendronotus albopunctatus* southward. Deep-water records are reviewed; 18 species, including *Colga pacifica*, *Bathydoris* sp., and *Chlamylla* sp., have been reported from Oregon waters as deep as 3000 m.

The systematics and occurrence of a few species previously reported from Oregon are reviewed and updated. *Melibe leonina*, not reported from the state since the mid-19th century, was recently observed in Yaquina Bay. The presence of *Aldisa sanguinea* in Oregon is confirmed, and one species, reported previously as the opisthobranch *Pleurobranchus* sp., was determined to be the prosobranch *Marsenina* sp.

Intertidal opisthobranchs were examined at three sites on the Oregon coast south of Cape Arago. Forty-three species were observed, including 41 from a 40 × 80 m area at Boardman State Park. The latter site, with its rough topography, numerous small caves, and abundance of seastars, supports one of the most diverse opisthobranch faunas known on the Oregon coast.

INTRODUCTION

GODDARD (1984) attempted to list all of the benthic opisthobranchs known from Oregon. Since then, only *Aplysia californica* Cooper, 1863, has been added to the fauna (PEARCY *et al.*, 1985; PEARCY & SCHOENER, 1987). The present paper describes new records, reports on the rich and previously undocumented opisthobranch fauna of the Oregon coast south of Cape Arago, and reviews deep-water records (most of which come from previously overlooked references). To further update GODDARD (1984), notes are presented on the systematics and occurrence of a few species already recorded from the state.

Owing to the presence of some less familiar genera, the deep-water species are listed systematically; otherwise, species are arranged alphabetically. Collecting sites are shown in Figure 1 and are listed with their latitude and longitude in Table 1.

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Species Not Previously Recorded from Oregon

An asterisk (*) before a species name indicates an extension of known geographic range; ranges are given only for those species so marked.

Acanthodoris rhodoceras Cockerell *in* Cockerell & Eliot, 1905
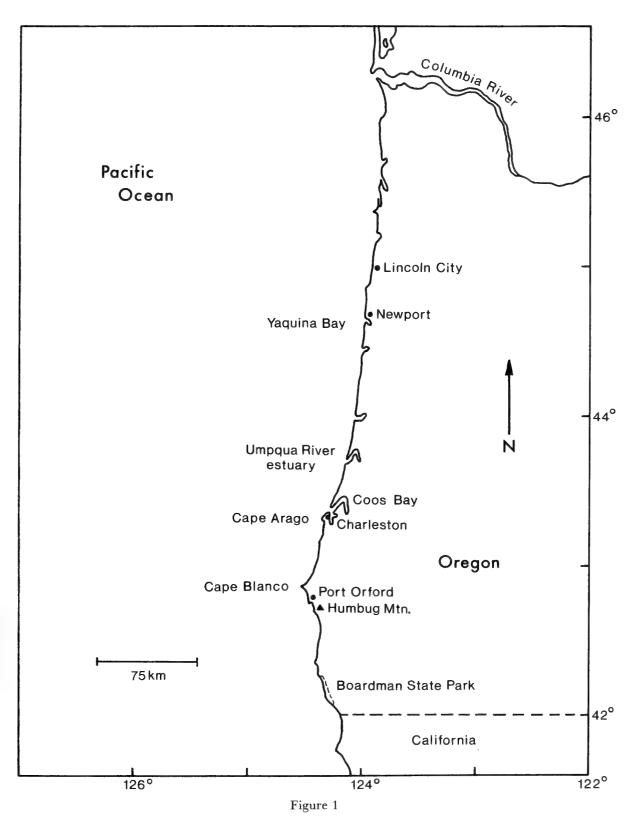
Cape Arago, Oregon (mouth of Humboldt Bay, California; JAECKLE, 1984) to Punta Cono, Baja California, Mexico (BERTSCH & AGUILAR ROSAS, 1984).

One specimen, 16 mm long, was found feeding on the encrusting ctenostomatous bryozoan *Alcyonidium* sp. on the underside of a boulder (approximately +0.3 m tide level) at North Cove, Cape Arago on 12 April 1987.

Acteocina harpa (Dall, 1871)

A single specimen of this minute bullomorph was found crawling on algae in a low intertidal pool at North Cove, Cape Arago, on 18 July 1985. The shell measured 4 mm in length.

Figure 1

Map of Oregon showing the location of some of the collecting sites.

Table 1

Location of collecting sites along the coast of Oregon.

Site	Latitude N	Longitude W
Mouth of the Columbia River	46°15'	124°00'
Yaquina Bay	44°37'	124°02'
Mouth of the Umpqua River	43°40'	124°11'
Charleston	43°20'	124°19'
Cape Arago	43°20'	124°22'
Cape Blanco	42°50'	124°33'
Port Orford	42°44'	124°29'
North end of Humbug Mountain State Park	42°42'	124°27'
North end of Boardman State Park	42°13'	124°22'

Cuthona lagunae (O'Donoghue, 1926)

North end of Boardman State Park, Curry County, Oregon (Palmer's Point, California; JAECKLE, 1984) to Punta Cabras, Mexico (Hamann, 1981, cited by BEHRENS, 1984:66).

Three individuals were observed at the north end of Boardman State Park on 11 July 1987; one of these was on the hydroid *Sertularella* sp. Despite good conditions and careful searching, *Cuthona lagunae* was not found during three other trips made between 1985 and 1989 to the same site at about the same time of year (see below, Observations on the Intertidal Opisthobranchs of Southern Oregon) and thus may be considered sporadic in occurrence there.

Dendronotus albopunctatus Robilliard, 1972

Charleston boat basin, Coos Bay, Oregon, and San Juan Islands, Washington. Previously known only from the San Juan Islands, Washington (ROBILLIARD, 1972).

One specimen, 28 mm long, was found at a depth of 2 m on a muddy bottom in the Charleston inner boat basin by Wendy Lou Manley on 11 April 1986.

Dendronotus albus MacFarland, 1966

Since 1983 I have found nine individuals, ranging in length from 2 to 25 mm, at Middle Cove, Cape Arago, and a single specimen at Boardman State Park. Most were found on the same hydroid species, *Abietinaria* sp., eaten by *Doto amyra* Marcus, 1961 (GODDARD, 1984). The identity of the minute specimens was confirmed after rearing them on this hydroid in the laboratory for a few weeks.

Dendronotus diversicolor Robilliard, 1970

One specimen, 33 mm long, of the white form of this species was observed in the low intertidal zone at the north end of Boardman State Park on 7 May 1989.

Doridella steinbergae (Lance, 1962)

Four specimens, 2–3 mm long, were found on 7 September 1989 feeding on colonies of the bryozoan *Mem-*

branipora membranacea that were growing on *Laminaria* sp. hanging from floating docks in Yaquina Bay. Despite careful searching, *Doridella steinbergae* has not been found on *M. membranacea* collected from Coos Bay during the past few summers and autumns.

Pleurobranchaea californica MacFarland, 1966

Port Orford, Oregon (near mouth of Klamath River, California; CHIVERS, 1967) to San Diego, California (CHIVERS, 1967).

One specimen, 220 mm long, was taken on 25 January 1985 from a commercial crab pot in waters about 35 m deep near Port Orford and delivered to the Oregon Institute of Marine Biology by Dale Bures.

Tenellia adspersa (Nordmann, 1845)

Coos Bay, Oregon (San Francisco Bay, California; STEINBERG, 1963) to Long Beach Harbor, California (CARLTON, 1979); and a global distribution, caused, at least in part, by introductions via shipping (ROGINSKAYA, 1970; CARLTON, 1979; THOMPSON & BROWN, 1984).

Numerous individuals and egg masses were found among the basal stolons of the hydrozoan *Tubularia crocea* from upper Coos Bay in August 1986 and August 1987. The egg masses, short-term lecithotrophic veliger larvae, and newly metamorphosed juveniles all closely matched those described and depicted by RASMUSSEN (1944).

Tenellia adspersa was probably introduced (via shipping) to Coos Bay (J. T. Carlton, personal communication).

Notes on Species Previously Recorded from Oregon

Aldisa sanguinea (Cooper, 1863)

Aldisa sanguinea usually possesses one or two dark spots on the midline of the dorsum between the rhinophores and the branchial plumes (McDONALD & NYBAKKEN, 1980; BEHRENS, 1980). All specimens previously reported from Oregon have lacked these spots (SOWELL, 1949; GODDARD, 1984), raising some question about their specific identity (GODDARD, 1984:145–146). Since 1983 I have observed over 18 individuals of *A. sanguinea*, many with one or two of these spots, at Good Witch, Middle, and North coves of Cape Arago.

Melibe leonina (Gould, 1852)

As described by SPHON (1972), the first record of *Melibe leonina* in Oregon (and, indeed, the first record of any species of opisthobranch from Oregon) was that of CARPENTER (1857). Apparently no records of this species in Oregon have been published since.

Numerous specimens of *Melibe leonina*, up to 60 mm long, were observed by Sarah Fryer and Robert Oswald on the sides of floating docks at Newport on Yaquina Bay on 9 October 1988. I maintained four of these in flow-through aquaria, where they laid egg masses a few centimeters in length similar to those described by HURST

(1967). However, the egg capsules in these egg masses contained 1–5 eggs, whereas HURST (1967:259) noted "15 to 25" eggs per capsule and "as few as 5." Small planktotrophic veligers hatched from one egg mass in 7–8 days at 12–15°C.

Marsenina sp.

SPHON (1972) reported a single specimen of "*Pleurobranchus* sp." that GODDARD (1984:Table 3) listed as a questionable species, owing to the lack of specific identification and its possible identity as *Berthella californica* (Dall, 1900) (which is known to occur at Cape Arago). Examination of Sphon's original specimen (Catalogue No. A.7066, Invertebrate Section, Natural History Museum of Los Angeles County) revealed it to be the lamellariid prosobranch *Marsenina* sp.

Tritonia diomedea Bergh, 1894

This species was erroneously listed as occurring at Cape Arago in GODDARD (1984:Table 3). In Oregon *Tritonia diomedea* has been collected from deep waters only (THOMPSON, 1971; MCCAULEY, 1972; PEREYRA & ALTON, 1972; and see below).

Deep-Water Records

In reviewing the benthic opisthobranchs known from Oregon, GODDARD (1984) overlooked four references containing significant records of opisthobranchs from the continental shelf, continental slope, and abyssal plain off Oregon. These references contain most of our knowledge about deep-water opisthobranchs off the coast of Oregon.

MCCAULEY (1972) summarized deep-water collections of epifaunal invertebrates from off the Oregon coast, including five species of nudibranchs from depths ranging from 25 to 3000 m. Specific collecting localities were not described. PEREYRA & ALTON (1972) reported eight species of opisthobranchs among samples of benthic invertebrates in depths ranging from 91 to 2103 m along a transect line extending south by southwest from the mouth of the Columbia River. BERTRAND (1971) found three species of cephalaspideans in his study of the infauna of the central Oregon continental shelf, between the mouth of the Umpqua River and Yaquina Bay (see Figure 1) in depths ranging from 75 to 450 m. RICHARDSON *et al.* (1977) collected eight species of opisthobranchs from depths of 10 to 100 m off the mouth of the Columbia River.

To my knowledge, only two other studies mention deep-water opisthobranchs from Oregon. THOMPSON (1971) examined five specimens of *Tritonia diomedea* (as *T. exsulans*) collected from 1000 to 1260 m "off the Oregon coast." These specimens were collected by personnel aboard Oregon State University research vessels from depths virtually identical to those given for this species by MC-CAULEY (1972) and thus are probably the same as those reported by McCauley. BELCIK (1975) examined collections in the Department of Oceanography at Oregon State

University and reported three species of nudibranchs from deep water. These were included in GODDARD's (1984) list of benthic opisthobranchs from Oregon. The specimens of *Bathydoris* sp. and *Tritonia* sp. documented by Belcik appear to be the same as those listed by MCCAULEY (1972).

Twenty species of opisthobranchs were found in the above studies in depths ranging from 10 to 3000 m. The 18 species identified at least to the level of order, and the depths at which they were collected, are listed in Table 2. In addition to providing significant bathymetric data, these records add seven species to the list of Oregon opisthobranchs compiled by GODDARD (1984:Table 3) and include one extension of known geographic range (see below).

PEREYRA & ALTON's (1972) record of *Colga pacifica* (as *Issena pacifica*) is the only record of this distinctive species in the northern Pacific since Bergh's description of the type specimen from 79 m near Unimak Island, Alaska (O'DONOGHUE, 1926; LEE & FOSTER, 1985). The species' geographic range (not discussed by PEREYRA & ALTON, 1972) is thus extended southeastward by approximately 2900 km. Pereyra and Alton's specimens of opisthobranchs were examined by Henning Lemche, and given Lemche's experience with specimens of *C. pacifica* from the North Atlantic (see JUST & EDMUNDS, 1985:60–61; PLATTS, 1985), the record is probably valid.

To my knowledge, the genus *Chlamylla* (see Table 2) has not been reported previously from the eastern Pacific. However, the taxonomic status of *Chlamylla* is unclear, and further work may reveal it to be a junior synonym of *Flabellina*, a genus well represented in the eastern Pacific (see MILLER, 1971:313; KUZIRIAN, 1978).

Observations on the Intertidal Opisthobranchs of Southern Oregon

Except for a single record of *Cuthona cocoachroma* from Cape Blanco (GODDARD, 1984:148), there are no previous records of opisthobranchs from the Oregon coast south of Cape Arago. Three rocky intertidal areas on this part of the coast were examined for benthic opisthobranchs between 1982 and 1989.

Cape Blanco: Cape Blanco is a low-elevation, exposed rocky headland with an intertidal zone dominated by wave-cut rock shelves, large boulders, and a few rock stacks. Long sandy beaches lie to the north and south. Two trips were made, one on 26 April 1982, the other on 19 August 1986.

Humbug Mountain State Park: Two wave-exposed boulder fields located between Rocky Point and Coal Point and just inside the north boundary of Humbug Mountain State Park were examined during a minus tide on 15 May 1987. Most of the boulders were partially buried in sand, limiting the amount of suitable habitat for opisthobranchs and their prey.

Boardman State Park: The study area measured approximately 40 × 80 m and was located in the low inter-

Table 2

Benthic opisthobranch mollusks collected from deep water off the coast of Oregon. Only species identified at least to the level of order are listed, and recent nomenclatural changes are incorporated. A plus sign (+) indicates a species not included in GODDARD's (1984) list of benthic opisthobranchs from Oregon.

Species	Depth range, meters[1]	Reference[2]
Order CEPHALASPIDEA		
Family ACTEONIDAE		
+*Rictaxis punctocaelatus* (Carpenter, 1864)	(75–450)	3
Family CYLICHNIDAE		
+*Acteocina culcitella* (Gould, 1852)	366	2, 3
+?*Acteocina* sp.	(10–100)	4
+*Cylichna attonsa* (Carpenter, 1864)	(10–450)	3, 4
Family GASTROPTERIDAE		
+*Gastropteron pacificum* Bergh, 1894	(10–100)	4
Family AGLAJIDAE		
Melanochlamys diomedea (Bergh, 1894)	(10–100)	4
Order NOTASPIDEA		
Family PLEUROBRANCHAEIDAE		
+*Pleurobranchaea californica* MacFarland, 1966	35	present study
Order NUDIBRANCHIA		
Suborder DENDRONOTACEA		
Family TRITONIIDAE		
Tritonia diomedea Bergh, 1894	640–1260	1, 2
Tritonia sp.	200–2086	1, 5
Tochuina tetraquetra (Pallas, 1788)	54	5
Suborder DORIDACEA		
Family BATHYDORIDIDAE		
Bathydoris sp.	2709–3000	1, 5
Family POLYCERIDAE		
+*Colga pacifica* Bergh, 1894		
(as *Issena pacifica* Iredale & O'Donoghue, 1923)	247	2
Family ARCHIDORIDIDAE		
Archidoris montereyensis (Cooper, 1863)	100	1
Unidentified dorid	247	2
Unidentified dorid	(10–100)	4
Suborder ARMINACEA		
Family ARMINIDAE		
Armina californica (Cooper, 1863)	25–200	1, 2, 4
Armina sp.	91	2
Suborder AEOLIDACEA		
Family FLABELLINIDAE		
+*Chlamylla* sp.	777	2

[1] If the depth range of a species was not available, then the depth range of the study (or combined ranges of more than one study) is given in parentheses.
[2] 1, McCAULEY (1972); 2, PEREYRA & ALTON (1972); 3, BERTRAND (1971); 4, RICHARDSON et al. (1977); 5, BELCIK (1975).

tidal zone 1.2 km north of the mouth of Houstenader Creek at the north end of Boardman State Park (42°13'22"N, 124°22'55"W). Although most of the neighboring shore is fully exposed to ocean swells, the study area is protected by outer rocks and a tall rock stack. Its topography is rough and irregular, consisting of large boulders, rock ridges, and tidepools and channels of variable depth. Small caves and overhangs, lined with luxuriant communities of sessile invertebrates, are numerous. Sea urchins were scarce.

Five trips, four during minus tides, were made to this site on the following dates: 2 July 1985, 11 July 1987, 17 July 1988, 11 October 1988 (not a minus tide), and 7 May 1989.

A total of 43 species of opisthobranchs were found on the southern Oregon coast, and 41 of these occurred at Boardman State Park alone (Table 3). Seventeen species were observed at each of the other localities. All but two of the 43 species were nudibranchs.

Table 3

Opisthobranchs observed intertidally on the coast
of Oregon south of Cape Arago, 1982–1989.

	Locality[1]		
Species	Board-man State Park	Humbug Moun-tain State Park	Cape Blanco
Acanthodoris hudsoni MacFarland, 1905	X		
Acanthodoris nanaimoensis O'Don-oghue, 1921	X		X
Aeolidia papillosa (Linnaeus, 1761)	X		
Aldisa sanguinea (Cooper, 1863)	X		
Ancula pacifica MacFarland, 1905	X	X	
Anisodoris nobilis (MacFarland, 1905)	X		
Archidoris montereyensis (Cooper, 1863)	X	X	X
Cadlina marginata MacFarland, 1905	X		X
Cadlina modesta MacFarland, 1966	X		
Catriona columbiana (O'Dono-ghue, 1922)	X	X	X
Cuthona abronia (MacFarland, 1966)		X	
Cuthona albocrusta (MacFarland, 1966)	X	X	
Cuthona cocoachroma Williams & Gosliner, 1979		X	X
Cuthona divae (Marcus, 1961)	X	X	X
Cuthona flavovulta (MacFarland, 1966)	X		
Cuthona fulgens (MacFarland, 1966)	X	X	
Cuthona lagunae (O'Donoghue, 1926)	X		
Dendronotus albus MacFarland, 1966	X		
Dendronotus diversicolor Robil-liard, 1970	X		
Dendronotus frondosus (Ascanius, 1774)	X	X	X
Dendronotus subramosus Mac-Farland, 1966	X		
Diaphana californica Dall, 1919	X		
Diaphorodoris lirulatocauda Mil-len, 1985	X		
Dirona albolineata Cockerell & Eliot, 1905	X		X
Dirona picta MacFarland *in* Cockerell & Eliot, 1905	X		
Discodoris heathi MacFarland, 1905	X		
Discodoris sandiegensis (Cooper, 1863)	X	X	X
Doto amyra Marcus, 1961	X	X	X

Table 3

Continued.

	Locality[1]		
Species	Board-man State Park	Humbug Moun-tain State Park	Cape Blanco
Doto columbiana O'Donoghue, 1921	X		X
Doto kya Marcus, 1961	X		
Eubranchus olivaceus (O'Dono-ghue, 1922)	X	X	
Eubranchus rustyus (Marcus, 1961)	X		
Flabellina trilineata (O'Donoghue, 1921)	X	X	X
Hallaxa chani Gosliner & Wil-liams, 1975	X		
Hermissenda crassicornis (Esch-scholtz, 1831)	X	X	X
Janolus fuscus O'Donoghue, 1924	X	X	X
Laila cockerelli MacFarland, 1905	X		
Onchidoris muricata (Müller, 1776)	X		
Placida dendritica (Alder & Han-cock, 1843)	X		
Rostanga pulchra MacFarland, 1905	X	X	X
Triopha catalinae (Cooper, 1863)	X	X	X
Triopha maculata MacFarland, 1905	X		X
Tritonia festiva (Stearns, 1873)	X		
Number of species per locality	41	17	17

[1] See Figure 1, Table 1, and text for specific localities.

The mean number of species I found (working alone, usually for 3 h) per minus tide at Boardman was 27.2 ($n = 4$; range, 23–30 spp.). The diversity of opisthobranchs observed here compares favorably with that at Middle Cove, Cape Arago, where, in an area of similar size and habitat complexity, I have twice found 29 species on a single low tide and where a total of 42 species have been observed (GODDARD, 1984, and unpublished data). However, this total was reached after 25 trips over an 8-yr period. A similar effort at Boardman would probably reveal even more species. The substratum at Boardman (composed primarily of tough graywacke sandstones dating from the Jurassic [BALDWIN, 1981; personal observations]) is harder and less susceptible to erosion than the Eocene sandstones at Cape Arago and may allow for the establishment of a more mature and complex encrusting community capable of supporting more species of opisthobranchs. In addition, juveniles of the seastars *Solaster dawsoni* and *Pycnopodia helianthoides* were more numerous at Boardman than at Middle Cove (personal observations). In the laboratory both of these species elicit escape re-

sponses by many nudibranchs, and occasionally capture and prey on them (FEDER, 1980; T. A. Wayne, personal communication; personal observations). Attacks by these seastars on nudibranchs (and on potential competitors of the nudibranchs) could be an additional factor maintaining the high diversity of nudibranchs at Boardman (*e.g.,* see PAINE, 1966; HUSTON, 1979).

Two opisthobranch species known from Cape Arago but conspicuously absent from Boardman are *Archidoris odhneri* and *Berthella californica.* At Cape Arago both species are most often observed among submerged boulders kept relatively barren of foliose algae by sea urchins, limpets, and chitons (GODDARD, 1984, and unpublished observations). The nature of this association is unknown, but this type of habitat is essentially nonexistent at Boardman, where seastars and other predators presumably suppress low-intertidal populations of herbivorous grazers.

Sixty-five percent (11/17) of the species of nudibranchs found at Humbug Mountain were predators of hydroids. This compares to 44 and 47% for Boardman and Cape Blanco respectively, where sponge- and bryozoan-feeding nudibranchs tended to be more common. Greater exposure of the boulders at Humbug Mountain to shifting sands, resulting in under-rock communities of hydroids and other early successional (or sand-resistant) species, probably explains the higher proportion of hydroid-feeding nudibranchs observed there (see McGUINNESS, 1987; BOERO, 1984; also SOUSA, 1979).

Hermissenda crassicornis was abundant at all three sites. All but two specimens (from Humbug Mountain) were of the variety possessing a bluish-white, longitudinal stripe on each ceras (see BEHRENS, 1980:93, lower photograph; McDONALD, 1983:201–202).

ACKNOWLEDGMENTS

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Temporary Northern Range Extension of the Squid *Loligo opalescens* in Southeast Alaska

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Abstract. This note reports a temporary northern extension of the range of the California market squid, *Loligo opalescens* Berry, 1911, to 58°N in Southeast Alaska and suggests that water temperatures influence the northern limits of this neritic squid.

The reported range of *Loligo opalescens*, Berry, 1911, the only loliginid in the northeastern Pacific, is from Baja California (28°N) to southern Southeast Alaska (55°N) (BERNARD, 1970; HIXON, 1983). Although the main commercial harvest comes from California, small commercial fisheries exist in Baja California, Oregon, and Washington (ROPER *et al.*, 1984). Potentially, commercial stocks exist in British Columbia (BERNARD, 1980) and Southeast Alaska (STREET, 1983).

Reports of *Loligo opalescens* in Southeast Alaska are sparse. REID (1961) found *L. opalescens* in the stomachs of chinook (*Oncorhynchus tshawytscha* Walbaum, 1792) and coho (*O. kisutch* Walbaum, 1792) salmon from Southeast Alaska in 1957–1958. *Loligo opalescens* was not subsequently reported in Alaska until 1980, prompting exploratory fishing around Prince of Wales Island in 1982 (STREET, 1983). During 1982, *L. opalescens* was found in stomachs of troll-caught salmon off the west coasts of Baranof and Yakobi islands (KARINEN *et al.*, 1985; WING, 1985).

Loligo opalescens was collected north of latitude 55°N on several occasions from 1982 through 1984 during research projects of the Auke Bay Laboratory and from stomachs of salmon caught by participants of the Alaska Troll Logbook Program (Figure 1, Table 1). The collections from Yakobi Island (58°N) are the most northerly

records for this species; the trawl catch west of the Myriad Islands (57°N) is the most northerly evidence of schooling; and the collection of egg capsules at Rowan Bay (56°N) is the most northerly observation of spawning.

The trawl catch of *Loligo opalescens* from west of the Myriad Islands is of interest because the number of specimens captured (>230) indicates that the sample was from a large school. These squid were classified as mature or immature (Table 2), based on the presence or absence of eggs or sperm (FIELDS, 1965); ca. 94% of the females had maturing ovaries and 61% of the males had spermatophores. Mantle lengths (ML) averaged 78.4 mm and 83.7 mm for males and females, respectively. These squid were captured at 126 m and at a bottom water temperature of 6.9°C.

Loligo opalescens spawns at water temperatures from 7°C (BERNARD, 1980) to 16°C (FIELDS, 1965). Water temperatures above 7°C occur in the southern portion of Southeast Alaska from March to December, with maximum temperatures of 13–16°C occurring in July and August (WILLIAMSON, 1965; JONES, 1978). Spawning is sporadic from December through September in British Columbia (BERNARD, 1980). Although *L. opalescens* spawns regularly in Barkley Sound (SHIMEK *et al.*, 1984), spawning may not occur annually at other British Columbia locations

Table 1

Loligo opalescens collected north of latitude 55° from 1982 through 1984.

Collection number*	Collection data			
	Samples	Date	Southeast Alaska location	Method, depth
	Live captures			
AB 82-20	335 egg capsules	21 July 1982	Rowan Bay, Kuiu Island 56°39.4'N, 134°15.5'W	Scuba diving, 12–15 m
AB 83-21	2 juveniles (57 & 87 mm ML)**	4 Aug. 1983	Port Conclusion, Baranof Island 56°15.8'N, 134°39.8'W	Trawl, 18–37 m on hard bottom
AB 84-54 NMML 454	230+ specimens (57–116 mm ML) (27 specimens are at AB, 63 at NMML; rest discarded)	4 May 1984	West of Myriad Islands 57°33.6'N, 136°22.3'W	Trawl, 126 m on hard bottom
AB 84-71	1 male (86 mm ML)	17 July 1984	Lisianski Inlet, east side Yakobi Island, 58°0.6'N, 136°28'W	Purse seine, 0–45 m
AB 84-72	1 juvenile (57 mm ML)	18 July 1984	Herbert Graves Island 57°41'N, 136°11'W	Purse seine, 0–45 m
	Stomach contents			
AB 83-47	2 juveniles (21 & 22 mm ML)	10 Apr. 1982	Whale Bay, Baranof Island 56°36.3'N, 135°2.5'W	Chinook salmon stomach
AB 83-48	1 adult (89 mm ML)	14 Apr. 1982	Whale Bay, Baranof Island 56°36.3'N, 135°2.5'W	Chinook salmon stomach
AB 83-49	1 adult (93 mm ML)	18 Aug. 1982	Surge Bay, Yakobi Island 57°59.7'N, 136°33.1'W	Coho salmon stomach
AB 83-50	1 adult (81 mm ML)	1 July 1983	Hoktaheen, Yakobi Island 58°4.4'N, 136°33.0'W	Chinook salmon stomach

* Collections held at the Auke Bay Laboratory, Auke Bay, Alaska (AB) or the National Marine Mammal Laboratory, Seattle, Washington (NMML).

** ML = dorsal mantle length.

(FIELDS, 1965). Frequency of spawning in southern Southeast Alaska is unknown.

The two periods during which *Loligo opalescens* has been documented in Southeast Alaska are associated with warmer than average waters: REID (1961) reported squids, including *L. opalescens,* as common in stomach contents (1.3–13.8%) of troll-caught chinook salmon during the strong 1957–1958 El Niño, and STREET (1983) collected *L. opalescens* in southern Southeast Alaska from 1980 to 1982 following a warming trend that began in 1970 (ROYER, 1985). The presence of *L. opalescens* as far north as Cross Sound in northern Southeast Alaska during 1983 and 1984 probably resulted from a combination of the 1982–1983 El Niño and the long-term warming trend. The possibility that this warming trend resulted in an overall increase in abundance of *L. opalescens* is consistent with observations in central California where successive warm years resulted in increased harvest (McINNIS & BROENKOW, 1979). Increased landings in Washington also occur during or following a strong El Niño (SHOENER & FLUHARTY, 1985). During the 1982–1983 El Niño, squid from the more southerly areas may have established small spawning populations along the coast from southern Baranof Island to Cross Sound. Although the specimens collected in 1984

from the Myriad Islands were in spawning condition, no specimens of *L. opalescens* have been collected during subsequent zooplankton and demersal fish surveys in the same general area. It appears, therefore, that permanent populations were not established.

Table 2

Sex, maturity, and size of *Loligo opalescens* collected west of the Myriad Islands, Southeast Alaska, 4 May 1984. Measurements made before preservation.

Sex and maturity	Mean dorsal mantle length (mm)	Number measured (n = 202)
Females	83.7	109
Mature	84.4	102
Immature	73.7	7
Males	78.4	93
Mature	82.0	57
Immature	72.6	36
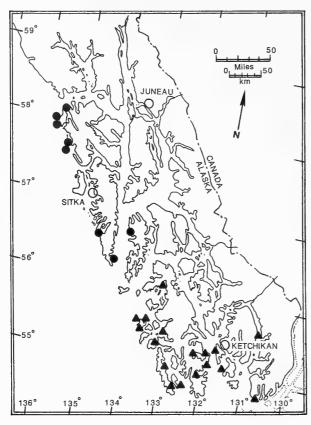
Figure 1

Capture localities of *Loligo opalescens* (closed circles) in northern Southeast Alaska and localities of observations (triangles) reported by STREET (1983) in southern Southeast Alaska.

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A Review of the Recent
Eastern Pacific Acanthochitoninae
(Mollusca: Polyplacophora: Cryptoplacidae)
with the Description of a New Genus, *Americhiton*

by

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Abstract. Recent species of the Acanthochitoninae in the eastern Pacific are reviewed. Members of the genus *Acanthochitona* include: *A. angelica* Dall, 1919, *A. avicula* (Carpenter, 1864), *A. exquisita* (Pilsbry, 1893), *A. ferreirai* Lyons, 1988, *A. hirudiniformis hirudiniformis* (Sowerby I, 1832), *A. hirudiniformis peruviana* (Leloup, 1941), and *A. imperatrix* Watters, 1981. A new genus, *Americhiton,* is created for *A. arragonites* (Carpenter, 1857), type species, and the western Atlantic species *A. andersoni* (Watters, 1981), *A. balesae* (Abbott, 1954), and *A. zebra* (Lyons, 1988).

INTRODUCTION

The family Cryptoplacidae, containing the two subfamilies Cryptoplacinae and Acanthochitoninae, includes diverse, predominantly tropical and subtropical chitons that have a confusing taxonomic history. Although this group is a significant component of most chiton faunas, the identification of even the most common species may be problematical. In recent years several attempts have been made to clarify the status of New World chitons including cryptoplacids. THORPE (1971) published an account of the eastern Pacific species and KAAS (1972) followed with Caribbean taxa. In 1980, I completed an unpublished Master's Thesis review of the family Cryptoplacidae in the New World utilizing scanning electron microscopy (SEM); my brief 1981 articles were extracted from that thesis. FERREIRA (1985) published a study of the chitons of Barbados in which he reached several incongruous and unfortunate conclusions on the family Cryptoplacidae. LYONS (1988a) also reviewed the Caribbean species of this family using SEM, and described six new species (one, however, was from the eastern Pacific), and corrected much of the confusion instituted by Ferreira. This report, modified from my 1980 thesis, covers the remaining eastern Pacific species.

The results of this study indicate that eight species and subspecies of Cryptoplacidae occur in the Recent of the eastern Pacific. All belong to the subfamily Acanthochi-toninae (the Caribbean *Choneplax lata* (Guilding, 1829) is the only New World member of the Cryptoplacinae). The eastern Pacific taxa are as follows:

Acanthochitona angelica Dall, 1919
Acanthochitona avicula (Carpenter, 1864)
Acanthochitona exquisita (Pilsbry, 1893)
Acanthochitona ferreirai Lyons, 1988
Acanthochitona hirudiniformis hirudiniformis (Sowerby I, 1832)
Acanthochitona hirudiniformis peruviana (Leloup, 1941)
Acanthochitona imperatrix Watters, 1981
Americhiton *arragonites* (Carpenter, 1857), gen. nov.

In strict accordance with ICZN rules (Art. 50 (a)), I have cited Pilsbry or Dall as the author of Carpenter's manuscript names where appropriate. Although this manuscript was the basis of much of their work on chitons, and its influence duly noted by subsequent workers, it was never published by Carpenter. Nevertheless, both authors gave credit to Carpenter for names and descriptions of taxa, and under ICZN Art. 50 (a), Carpenter could be considered the "some other person . . . alone responsible both for the name and for satisfying the criteria of availability other than publication," and as such "then that person is the author of the name." Numerous workers have not resolved this problem to their satisfaction and have cited these species as "Carpenter *in* Dall" or "Car-
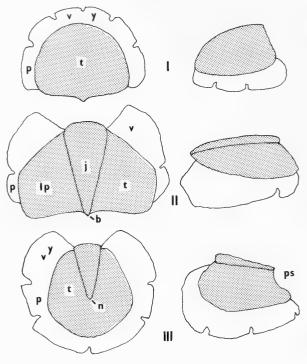
Figure 1

Shell plate morphology of *Acanthochitona*. I, anterior valve; II, intermediate valve; III, posterior valve; t, tegmentum; v, articulamentum; lp, latero-pleural areas; j, jugum; b, beak; n, mucro; y, apophyses; p, insertion plates; ps, post-mucronal slope.

Figure 2

Hypothetical pustule morphology. M, macresthete; ppm, premacresthete micresthetes; pps, prepustular slope. The growing edge is to the left.

penter *in* Pilsbry." However, I feel that Dall and Pilsbry contributed enough to the description and illustration of Carpenter's species to warrant authorship, and Carpenter is not considered the author for these names in this review.

MATERIALS AND METHODS

SEM studies were conducted at the University of Rhode Island during 1976–1980 under the guidance of Dr. R. C. Bullock, who, along with E. Leloup, first emphasized the taxonomic importance of tegmental microstructure. All specimens were sonically cleaned, desiccated, and coated with gold-palladium prior to observation. Details of the procedure used to examine these specimens may be found in BULLOCK (1988).

ABBREVIATIONS USED IN TEXT

AJF—Private collection, now housed at CASIZ, of the late A. J. Ferreira; AMNH—American Museum of Natural History, New York; ANSP—Academy of Natural Science, Philadelphia; BMNH—British Museum (Natural History), London; CASIZ—California Academy of Sciences, San Francisco; DMNH—Delaware Museum of Natural History, Greenville; GTW—Private collection of G. T. Watters, Ohio State University; MCZ—Museum of Comparative Zoology, Cambridge; LACM—Natural

History Museum of Los Angeles County Museum; OSUM—Museum of Zoology, Ohio State University; RCB—Private collection of R. C. Bullock, University of Rhode Island; RMNH—Rijksmuseum van Natuur-Lijke Historie, Leiden; SDMNH—San Diego Museum of Natural History; UMMC—Department of Zoology, University of Miami, Coral Gables; USNM—National Museum of Natural History, Washington, D.C.

TAXONOMIC CHARACTERS

Valve Morphology

In *Craspedochiton* Shuttleworth, 1853, the tegmentum topography is similar to the ischnochitonid condition in possessing central and lateral areas. However, in all New World Acanthochitoninae these regions have lost their identity and usually are referred to as the combined latero-pleural areas. In most Acanthochitoninae the jugum is well-differentiated, although it may be less so in crypto-placines, *Craspedochiton,* and related genera. The anterior valve lacks these areas and generally is of little taxonomic importance. The posterior valve is thought to be the result of the fusion of a terminal valve, much like the anterior one, and a pre-existing intermediate valve (BERGENHAYN, 1930; STAROBOGATOV & SIRENKO, 1978), but in most cases the demarcation between these two fused valves is obscured. The posterior apex of the jugum of this fused intermediate valve persists as a distinct region on the posterior valve and is referred to as the mucro. The area posterior to the mucro is the post-mucronal slope, and its outline in profile has been used in taxonomic schemes. These morphological regions are illustrated in Figure 1.

The dominant tegmental sculpturing in the family is pustules; these correspond to esthete bodies imbedded within the pustules. Two types of esthetes of uncertain function occur in the Cryptoplacidae, and are separated here on the basis of size into macresthetes and micresthetes (Figure 2). The position of the esthetes on the pustule is of taxo-
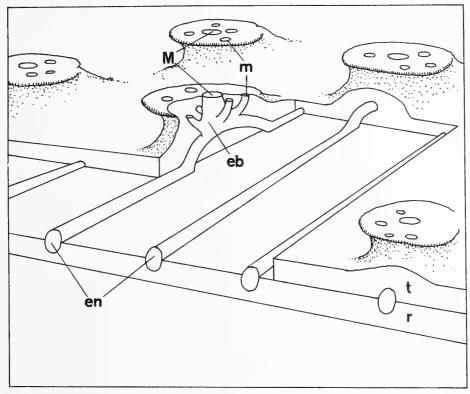
Figure 3

Esthete innervational system: diagrammatic cross-section through valve viewed from anterior growing edge. t, tegmentum; r, articulamentum; M, macresthetes; m, micresthetes; eb, esthete body; en, esthete nerves.

nomic importance. Figures 3–8 illustrate the morphology of these pustules and the relationship between the esthetes and the valve.

Girdle Elements

Cryptoplacids as a group have spiculose girdle elements, although in *Craspedochiton* these elements are flattened and scale-like. The dorsum of the girdle is covered with one or more types of spicules, which may be of taxonomic importance. Spicule types vary in sculpture (smooth or longitudinally striated), length, shape (straight or bent), and cross-sectional profile (round or flattened). In this study the term monomorphic is used to denote dorsal spicules of all one type; bimorphic refers to two distinct types of dorsal spicules that differ in any of the above regards. The determination of spicule types often requires the use of SEM or careful light microscopy examinations; gross morphological comparisons have sometimes led to erroneous conclusions (*e.g.*, FERREIRA, 1985). An example of dorsal elements is shown in Figure 9.

Cryptoplacids typically have 18 sutural tufts, one per side at the articulation of each pair of valves and four along the anterior margin of valve I. The spicules composing these tufts are usually straight (curled in *Choneplax* Dall, 1882) and unsculptured, and vary in number from three or four to hundreds per tuft. The tufts can be "fanned-out" or gathered together by the animal, and there is evidence that some species can partially withdraw the tufts into the girdle. Generally, variations in the tuft spicules are of limited taxonomic importance.
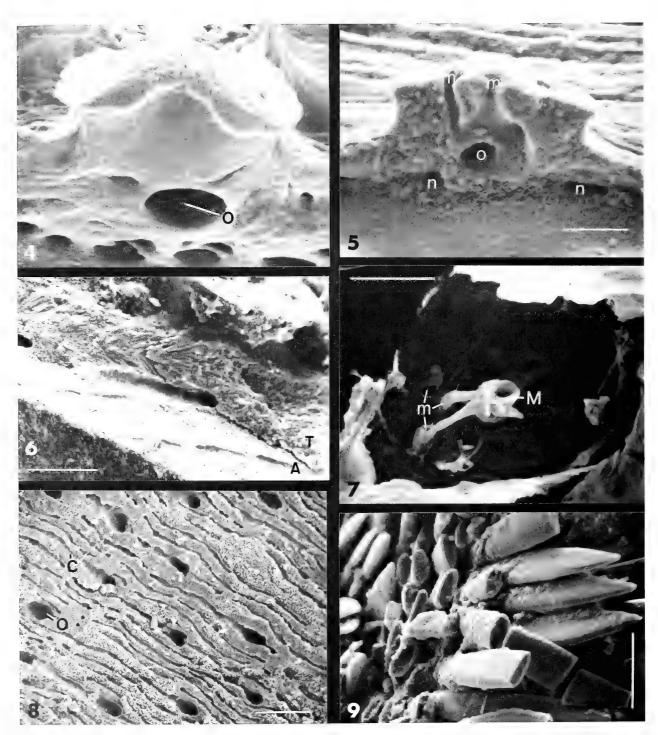
Dorsal elements may be mono- or bimorphic, straight or bent, and often sculptured with longitudinal striations. In *Acanthochitona* these elements are typically spiculose; in the cryptoplacines they are club-shaped; and in *Craspedochiton*, scale-like. Dorsal elements appear to be of taxonomic importance at the generic and specific levels.

The margin of the girdle is bounded by a fringe of spicules; these are usually flattened, monomorphic elements of little taxonomic importance.

The ventral side of the girdle is covered by small, flattened, monomorphic spicules, also of little taxonomic importance. These spicules radiate outward from the median of the animal.

Radula

The radula of chitons is a complex structure, containing 15 discrete teeth per row plus additional outer, small laterals. The largest tooth, the major lateral, has a denticle cap composed of a magnetite compound. Various degrees of taxonomic importance have been assigned to the radulae of chitons by workers, ranging from the early classifications of Thiele, based almost exclusively on radulae, to those of

Explanation of Figures 4 to 9

Figures 4–9. Cryptoplacid microstructures: valves and girdle.

Figure 4. *Choneplax lata* (Guilding, 1829), incompletely formed pustule at growing edge of valve. o, esthete body cavity in pustule (scale = 25 μm).

Figure 5. *Americhiton andersoni* (Watters, 1981), incompletely

formed pustule at growing edge of valve. m, micresthetes; n, esthete nerve canals; o, esthete body cavity (scale = 20 μm).

Figure 6. *Acanthochitona hirudiniformis hirudiniformis* (Sowerby I, 1832), fractured valve showing juncture of articulamentum (A) and tegmentum (T) with esthete nerve canals sandwiched between them (scale = 50 μm).

Bergenhayn, whose work on fossil chitons necessarily excluded that element. In this study, as in that of BULLOCK (1988), only the denticle caps, which are easily dislodged and observed, were examined in detail. My feeling is that in the Cryptoplacidae, the radular denticle caps are too variable to be used as a species-level diagnostic, and are only marginally useful at the generic level. Representative denticle caps are illustrated for several New World species in Figures 85–93. The denticle caps of all cryptoplacids so far examined by me are tridentate, each having a medial "peg" and occasionally also possessing a smaller, lateral one.

SYSTEMATIC TREATMENT

Class Polyplacophora Gray, 1821

Order Neoloricata Bergenhayn, 1930

Suborder Acanthochitonina Bergenhayn, 1930

Family CRYPTOPLACIDAE H. &. A. Adams, 1858

Description: Small to large in size (to 10 cm in length). Tegmental sculpture of pustules or coalesced pustules, lateral and central areas weakly or not at all defined, jugal area often distinct. Jugal sinus wide and deep. Valves not overlapping in adults of some genera. Pustules containing one or more esthete bodies; esthetes present between pustules in some genera. Apophyses usually extensive and relatively thin. Intermediate valves with one slit per side; anterior valve generally with five slits; posterior valve with two or more slits, often irregularly disposed. Girdle minutely to coarsely spiculose.

Remarks: This family displays a wide range in tegmental reduction and vermiformity, and many authors have advocated the division of these chitons into two families, the Acanthochitonidae (or Cryptoconchidae) and the Cryptoplacidae. However, the presence of intermediate genera such as *Choneplax* Dall, 1882, and *Meturoplax* Pilsbry, 1894, indicates that separation into separate families is unwarranted.

Subfamily ACANTHOCHITONINAE Pilsbry, 1893

Description: Small to moderate sized species. Sculpture of pustules, rarely coalesced into ribs, jugal area well-defined. Esthetes absent from tegmentum between pustules in all species studied. Articulamentum of posterior valve with two widely spaced slits (weak interslits occasionally present); area between slits occasionally concave. Girdle spiculose.

Remarks: This subfamily contains the following genera: *Acanthochitona* Gray, 1821, *Bassethullia* Pilsbry, 1928, *Craspedochiton, Cryptoconchus* Burrow, 1815, *Meturoplax* Pilsbry, 1894, *Notoplax* H. Adams, 1861, and **Americhiton** gen. nov.

A fossil record is known only for *Acanthochitona avicula,* which BERRY (1922) records from the Pleistocene of Santa Monica, California. I have not seen this specimen and cannot confirm its identification.

Genus *Acanthochitona* Gray, 1821

Acanthochitona GRAY, 1821:234. Type by monotypy, *Chiton fascicularis* Linnaeus, 1767; VAN BELLE, 1983:140–142 (synonymy).

Type species: *Chiton fascicularis* Linnaeus, 1767, by monotypy.

Diagnosis: Tegmentum sculptured with flat to concave pustules, no radial ribbing on any valve, no delineation between central and lateral areas. Jugum well-defined, smooth, or longitudinally striated. Macresthetes and/or micresthetes present on pustules and jugum but absent in interpustular spaces. Esthete innervational system sandwiched between tegmentum and articulamentum, myostracum palleale apparently absent or very reduced. Articulamentum moderately extensive. Slit formula 5-1-2+. Girdle broad relative to most chitons, encroaching on tegmentum; dorsum with dense, pointed spicules. Sutural tufts usually well-developed, marginal fringe present and conspicuous. Ventral side of girdle with fine daggerlike spicules.
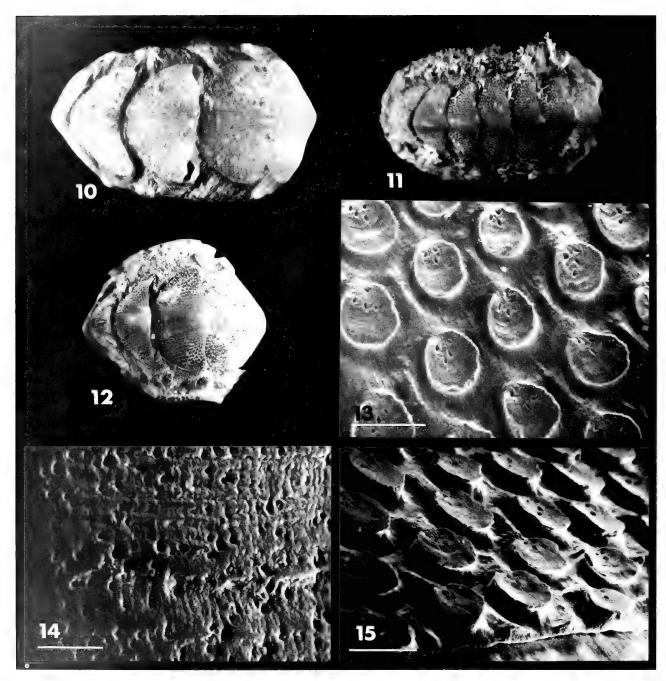
Remarks: The tegmental layer of *Acanthochitona s.s.* is very thin relative to that found in other studied chitons and the valves seem to lack a myostracum palleale. In the Chitoninae, this layer contains the esthete innervational system (LAGHI & RUSSO, 1979) and its absence in the acanthochitons results in the nerves being sandwiched between the tegmentum and articulamentum (this may be true of the family as a whole). The innervational system leaves its position on the tegmentum-articulamentum interface and enters the tegmentum to give rise to the esthete body proper. The typically pustulose sculpture is the direct result of the presence of these esthetes and simply represents the minimal tegmental covering over the esthete bod-

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Figure 7. *Acanthochitona fascicularis* (Linnaeus, 1767), internal view of decalcified valve pustule. M, central macresthete; m, branching micresthetes (scale = 25 μm).

Figure 8. *Acanthochitona astriger* (Reeve, 1847), internal view of tegmentum with articulamentum removed. Esthete nerves travel

in canals (c) between tegmentum and articulamentum until they penetrate tegmentum to form esthetes. o, esthete body cavity (scale = 100 μm).

Figure 9. **Americhiton** *andersoni* (Watters, 1981), dorsal girdle elements (scale = 100 μm).

Explanation of Figures 10 to 15

Figures 10–15. *Acanthochitona angelica* Dall, 1919.

Figure 10. Holotype of *Acanthochitona angelica* Dall, 1919, Bahía de Los Angeles, Baja California, Mexico (USNM) (11 mm, curled).

Figure 11. Paratype of *Acanthochitona jacquelinae* Smith & Ferreira, 1977, Academy Bay, Isla Santa Cruz (Indefatigable Id.), Galápagos Ids., Ecuador (AJF) (5 mm).

Figure 12. Isla Isabella, Galápagos Ids., Ecuador (ANSP) (6 mm, curled).

Figure 13. Dorsal view of pustules, Paratype of *Acanthochitona jacquelinae* Smith & Ferreira, 1977, Academy Bay, Isla Santa Cruz (Indefatigable Id.), Galápagos Ids., Ecuador (AJF) (scale = 100 μm).

Figure 14. Dorsal view of jugum, María Magdalena Id., Mexico (AMNH) (scale = 100 μm).

Figure 15. Oblique view of pustules, Paratype of *Acanthochitona jacquelinae* Smith & Ferreira, 1977, Academy Bay, Isla Santa Cruz (Indefatigable Id.), Galápagos Ids., Ecuador (AJF) (scale = 100 μm).

ies (Figure 3). In *Craspedochiton, Notoplax, Meturoplax,* and the Cryptoplacinae, micresthetes also are found between the pustules, resulting in a thicker layer of tegmental coverage. The pustules of these groups support more esthete bodies and are convex in surface relief; in *Acanthochitona s.s.* the pustules are concave and rarely contain more than two macresthetes. The well-defined jugal region of *Acanthochitona* may be derived from a coalescing of pustules along the dorsal ridge. This smooth, fortified region may facilitate movement and resist crushing as these chitons move on the undersurfaces of rocks and shells. Some genera, such as *Craspedochiton,* still possess pustules in this region.

GRAY (1821) was the first worker to separate acanthochitons from *Chiton,* listing *Chiton fascicularis* Linnaeus, 1767, as his only example. Because the name was published in an obscure journal (at least to malacologists), it remained largely unnoticed, and the most widely accepted name became *Acanthochites* Risso, 1826; indeed, GRAY (1843) adopted a misspelling of *Acanthochites* rather than his own *Acanthochitona.* HERRMANNSEN (1846), and many of those subsequent authors who did employ Gray's name, unnecessarily emended it to conform to the endings of other chiton taxa in use at that time: *Chiton, Ischnochiton, Enoplochiton, etc.* ASHBY (1922:9) pointed out that "acantho" and "chiton" are both masculine and regarded *Acanthochitona* as a "mongrel word." However, GRAY's (1821) spelling does not constitute an incorrect original spelling and should not be emended (see ICZN Art. 32, and Iredale, 1915). *Aristochiton* Thiele, 1910, is a synonym of *Craspedochiton s.l.,* not of *Acanthochitona* as stated by A. G. SMITH (1960).

Acanthochitona fascicularis complex

This group of species is characterized by its having proportionately broader, rectangular intermediate valves than those of the other eastern Pacific Acanthochitoninae, the *Acanthochitona hirudiniformis* complex, which tend to be more hexagonal in outline. The mucro is typically central and prominent, the sculpture is of oval to teardrop-shaped pustules, and the jugum is smooth or striated. The dorsum of the girdle may be covered with fine or coarse spicules; the sutural tufts are composed of fairly stout elements, fewer in number than in the *A. hirudiniformis* complex. This is a widespread complex including the common species *A. fascicularis* (Linnaeus, 1767), *A. crinita* (Pennant, 1777), and *A. zelandica* (Quoy & Gaimard, 1835).

Acanthochitona angelica Dall, 1919

(Figures 10–17, 28–30)

Acanthochitona angelica DALL, 1919:515; KEEN, 1958:518; PARKER, 1964:151, 166; THORPE, 1971:866; ABBOTT, 1974:407; A. G. SMITH, 1977:217, 254; KAAS & VAN BELLE, 1980:8; WATTERS, 1981b:173; pl. 1e–g; pl. 4e.; LYONS, 1988b:150; SKOGLUND, 1989:87.
Acanthochitona jacquelinae SMITH & FERREIRA, 1977:83, 93–
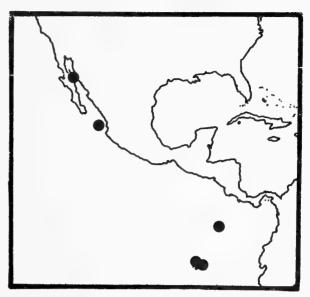
Figure 16

Distribution of *Acanthochitona angelica* Dall, 1919.

95; figs. 18, 19; WATTERS, 1981b:173; KAAS & VAN BELLE, 1980:67; FINET, 1985:11; SKOGLUND, 1989:88.
Acanthochitona shaskyi FERREIRA, 1987:47–52; figs. 8–12; SKOGLUND, 1989:88.
"*Acanthochitona* cf. *A. avicula* (Carpenter)": SMITH & FERREIRA, 1977:95; figs. 20, 21; FINET, 1985:11.
?*Acanthochitona* cf. *A. angelica* (Dall): McLEAN, 1961:473.
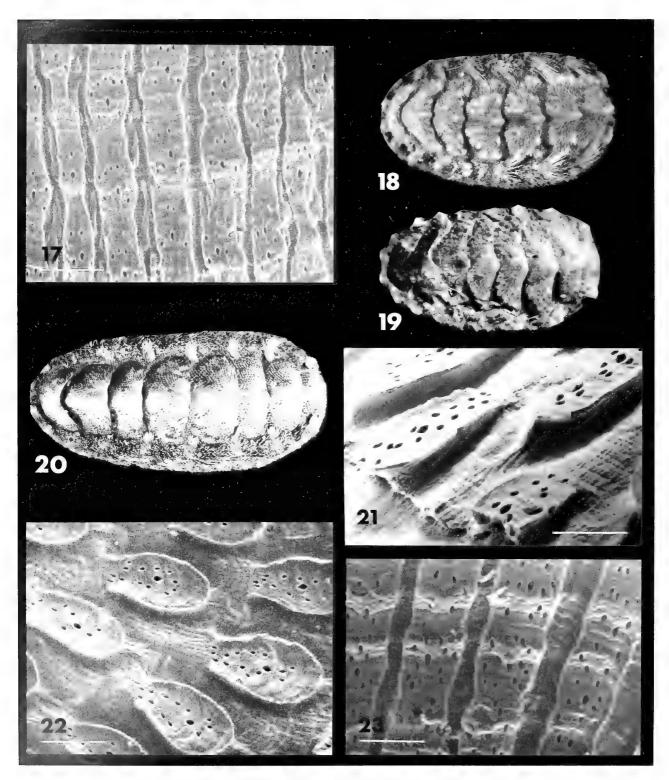
Type material: *Acanthochitona angelica* Dall, 1919. Holotype: USNM 110346.

Acanthochitona jacquelinae Smith & Ferreira, 1977. Holotype: CASIZ 967. Paratypes: 66 specimens, depositories unspecified. Type locality: Isla Coamaño (Jensen Id.), Galápagos Ids., in 40–60 m on broken coralline bottom.

Acanthochitona shaskyi Ferreira, 1978. Holotype: CASIZ 061094. Paratypes: LACM 2125; SDMNH 34359; USNM 859008; D. R. Shasky coll.; Ferreira coll. Type locality: Chatham Bay, Cocos Id., Costa Rica, in 46–69 m.

Type locality: Bahía de Los Angeles, Baja California, Mexico.

Description: Largest specimen seen, 15 mm in length. Tegmentum of intermediate valves much wider than long, moderately arched, not carinated. Beaks not prominent, posterior borders of valves nearly straight. Jugum smooth or cut with incised lines into 7–10 longitudinal striations. Jugal macresthetes arranged in longitudinal rows, each accompanied by 2–7 micresthetes. Latero-pleural areas finely pustulose, pustules oval or slightly teardrop-shaped. Each pustule bearing one macresthete located acentrically towards beak with 2–4 micresthetes confined to premacresthete area. Tegmentum uniformly orange, orange-red, brownish-red, green, white, or mottled with these colors;

Explanation of Figures 17 to 23

Figure 17. *Acanthochitona angelica* Dall, 1919. Dorsal view of jugum, Paratype of *Acanthochitona jacquelinae* Smith & Ferreira, 1977, Academy Bay, Isla Santa Cruz (Indefatigable Id.), Galápagos Ids., Ecuador (AJF) (scale = 100 µm).

Figures 18–23. *Acanthochitona avicula* (Carpenter, 1864).

Figure 18. Ensenada, Baja California, Mexico (GTW) (13 mm).

Figure 19. Syntype of *Acanthochites avicula* Carpenter, 1864,

adjacent groups of valves may differ in color from other groups on same specimen.

Apophyses variable in degree of extension. Slit formula 5-1-2. Articulamentum white or white tinged with pink or orange-red towards the beak.

Girdle dorsum velvety, with bimorphic elements composed of two distinct sizes of bent spicules, both at least distally striated. Dorsum colored uniformly orange-red, dark red, greenish, white, lavender, blue, or mottled with these colors. Sutural tufts and marginal fringe well-developed, colored translucent white, yellow, blue-green, blue, or lavender.

Distribution: Gulf of California to Panama and the Galápagos Ids. This is apparently an offshore species, found to at least 50 m.

Material examined: MEXICO: BAJA CALIFORNIA: Bahía de Los Angeles (USNM); TRES MARIAS ISLANDS: María Magdelina Id. (AMNH). ECUADOR: GALÁPAGOS ISLANDS: Isla Isabella (Albemarle Id.) (ANSP); Isla Santa Cruz (Indefatigable Id.), Bahía de la Academia (AJF).

Remarks: This species has been synonymized with *Acanthochitona avicula* as a result of the taxonomic confusion surrounding the New World *Acanthochitona*. In his "Descriptions of new species of chitons from the Pacific coast of America," DALL (1919) introduced some 36 chiton species, nearly one-third of which are considered junior synonyms today. Most were insufficiently described and none was illustrated, a factor that was to render the systematics of West Coast chitons unstable for years to come. Concerning *A. angelica,* DALL (1919:515) stated that "from *A. avicula* Carpenter, it is distinguished by its more central mucro, its generally larger valves and narrower girdle." The description of *A. angelica* contained little information of a diagnostic nature and the species apparently has not been recognized as distinct, except by myself (WATTERS, 1981b). THORPE (1971), ABBOTT (1974), PUTMAN (1980), and KAAS & VAN BELLE (1980) all conjectured that *A. angelica* was synonymous with *A. avicula,* a conclusion that is not supported by the present data. Although A. G. SMITH (1977) was correct in saying that the sculptural differences and color patterns of *A. angelica* are well within the limits of the variation exhibited by *A. avicula,* both he and Dall failed to recognize the more salient differences in girdle ornamentation.

SMITH & FERREIRA (1977) described a new species from the Galápagos Ids., *Acanthochitona jacquelinae,* and Fer-
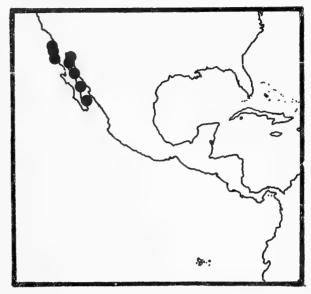
Figure 24

Distribution of *Acanthochitona avicula* (Carpenter, 1864).

reira kindly supplied me with paratypes. An examination of this material has revealed that *A. jacquelinae* is conspecific with *A. angelica.* The only apparent difference between the two is the smaller average size of the Galápagos specimens. SMITH & FERREIRA's (1977) observation that the sutural tufts are "unusually prominent for such a small sized chiton" (p. 93) would seem to indicate that the specimens are not mature. This is in keeping with my observation that in juvenile acanthochitons the sutural tufts are disproportionately larger than in adults.

In the same paper SMITH & FERREIRA (1977) described and illustrated specimens of "*Acanthochitona* cf. *A. avicula*" (p. 95, figs. 20, 21), also from the Galápagos Ids. From their photographs, their description of the jugal striations, and the "very small size of the spicules," these specimens are probably adults of *A. angelica.* They are careful to point out the differences in the girdle between *A. avicula* and their "Galápagos population" (*i.e., A. angelica*). It is perplexing that SMITH (1977), having seen Dall's type of *A. angelica,* did not recognize the differences in girdle ornamentation between *A. angelica* and *A. avicula,* but later, with Ferreira, carefully documented this difference in the descriptions of *A. jacquelinae* and "cf. *A. avicula.*" No mention of *A. angelica* was made in the latter paper.

←
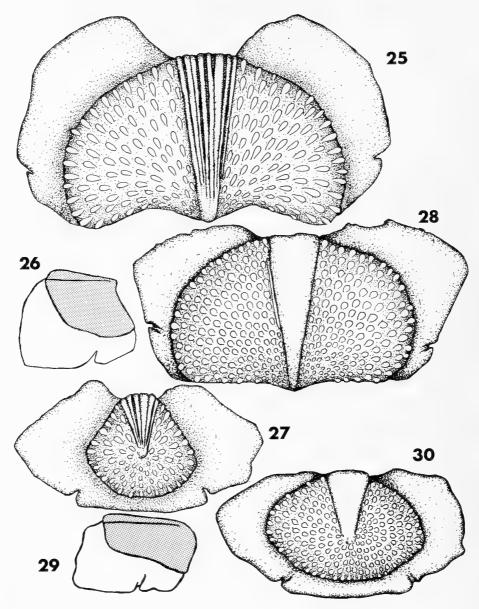
Catalina Id., California, USA (BMNH) (4.3 mm; partially disarticulated).

Figure 20. Lectotype of *Acanthochites avicula* variety *diegoensis* Pilsbry, 1893, San Diego, California, USA (ANSP) (19 mm).

Figure 21. Oblique view of pustules, Ensenada, Baja California, Mexico (GTW) (scale = 100 μm).

Figure 22. Dorsal view of pustules, Ensenada, Baja California, Mexico (GTW) (scale = 100 μm).

Figure 23. Dorsal view of jugum, Ensenada, Baja California, Mexico (GTW) (scale = 100 μm).

Explanation of Figures 25 to 30

Figures 25–27. *Acanthochitona avicula* (Carpenter, 1864), Agua de Chale, Baja California, Mexico (AMNH).

Figure 25. Intermediate valve VII (3.4 mm width).

Figure 26. Posterior valve profile.

Figure 27. Posterior valve (3 mm width).

Figures 28–30. *Acanthochitona angelica* Dall, 1919, María Magdalena Id., Tres Marías Ids., Mexico (AMNH).

Figure 28. Intermediate valve VII (3.8 mm width).

Figure 29. Posterior valve profile.

Figure 30. Posterior valve (2.7 mm width).

FERREIRA (1978) described *Acanthochitona shaskyi* from Cocos Id. He compared it with *A. jacquelinae*, finding minor differences in girdle elements and posterior valve profile. However, that species falls within the range of variation of *A. angelica*.

Acanthochitona angelica is the eastern Pacific cognate of the western Atlantic *A. pygmaea* (Pilsbry, 1893) and *A.*

venezuelana Lyons, 1988. From *A. pygmaea*, it differs in having dorsal girdle elements of two distinct sizes, both striated; in *A. pygmaea* these elements are of various lengths and are smooth. LYONS (1988a) does not mention any sculpture on the bimorphic spicules of *A. venezuelana* and compares it with *A. avicula*; however, as mentioned, *A. venezuelana* is more closely related to *A. angelica*. From *A.*

avicula, A. angelica differs in having a velvety girdle of very fine spicules rather than coarse, strongly curved elements, and in the absence of elongated pustules on the latero-pleural areas. *Acanthochitona imperatrix* can be differentiated by its wide, flat, and smooth jugum. As with most New World acanthochitons that typically possess a striated jugum, occasional specimens may be encountered in which this structure is smooth.

Acanthochitona avicula
(Carpenter, 1864)

(Figures 18–27, 88)

Acanthochites avicula CARPENTER, 1864:612, 650; CARPENTER, 1866:211; COOPER, 1867:23; CARPENTER, 1872:98, 136; PILSBRY, 1893b:24; NIERSTRASZ, 1905:60.

Acanthochiton avicula (Carpenter): DALL, 1879a:299; pl. 4, fig. 38; DALL, 1879b:81; pl. 4, fig. 38; LELOUP, 1941:3, 9; FISCHER, 1978:37.

Acanthochitona avicula (Carpenter): DALL, 1919:515; BERRY, 1922:456, 457; STRONG, 1923:43; I. S. OLDROYD, 1927:318, 319; STEINBECK & RICKETTS, 1941:549; BURCH, 1946:19; SMITH & GORDON, 1948:206; PALMER, 1958:21, 31, 43, 53, 286; pl. 32, fig. 4; BURGHARDT & BURGHARDT, 1969:9; pl. 1, fig. 1; THORPE, 1971:866; fig. 11; KAAS, 1972:47; ABBOTT, 1974:407; A. G. SMITH, 1977:254; SMITH & FERREIRA, 1977:94, 95; HOUSTON, 1980:195, 196; fig. 9.230; KAAS & VAN BELLE, 1980:13; WATTERS, 1981b:173; pl. 1h–j; pl. 4c, d; PUTMAN, 1982:366; LYONS, 1988a:97, 98, 112, 113; fig. 81; LYONS, 1988b:150; SKOGLUND, 1989:87.

Acanthochites avicula variety *diegoensis* PILSBRY, 1893b:25; pl. 12, figs. 52–54; NIERSTRASZ, 1905:58, 60; KAAS & VAN BELLE, 1980:38.

Acanthochiton avicula variety *diegoensis* (Pilsbry): LELOUP, 1941:3, 9.

Acanthochites diegoensis Pilsbry: T. S. OLDROYD, 1911:73.

Acanthochitona diegensis [*sic*] (Pilsbry): DALL, 1919:515; LOWE, 1935:32.

Acanthochitona diegoensis (Pilsbry); I. S. OLDROYD, 1927:318; BURCH, 1946:19; BURGHARDT & BURGHARDT, 1969:9; ABBOTT, 1974:407.

Acanthochites diegensis [*sic*] Pilsbry: STEINBECK & RICKETTS, 1941:548.

Acanthochitona avicula variety *diegoensis* (Pilsbry): WATTERS, 1981b:173; pl. 4d.

Acanthochitona arragonites variety *diegoensis* (Pilsbry): I. S. OLDROYD, 1927:318.

Non Acanthochitona cf. *avicula* "Carpenter," FINET, 1985:11 [=*Acanthochitona angelica* (Dall, 1919)].

Type material: *Acanthochites avicula* Carpenter, 1864. Holotype: Redpath Museum, No. 72.

Acanthochites avicula variety *diegoensis* Pilsbry, 1893. Lectotype: by subsequent designation of WATTERS (1981b), ANSP 349330. Type locality: San Diego, California, USA.

Type locality: Catalina Id., California, USA.

Description: Largest specimens seen, 20 mm in length. Tegmentum of intermediate valves wider than long, flattened, not carinated. Beaks prominent, jugum moderately wide, cut with deeply incised lines into 8–12 longitudinal

striations. Each jugal macresthete accompanied by 8–12 microsthetes; macresthetes on one striation not aligned with those on another. Latero-pleural areas sculptured with numerous, very elongate, teardrop-shaped pustules, with number of pustules and distance between them varying considerably between specimens. Each pustule bearing one macresthete located acentrically towards prepustular slope with 5–10 microsthetes, not confined to premacresthete area. Mucro varying in position from slightly anterior to posteriorly acentric, prominent, postmucronal slope steep and concave. Tegmentum whitish, variegated with brown, green, gray, and black; pustules often of different color than background tegmentum.

Apophyses well-developed. Slit formula (5–6)-1-2. Articulamentum white tinged with green towards the beak.

Girdle dorsum ornamented with coarse, bent spicules curving towards median, interspersed with smaller, curved spicules that become predominant towards valves. Larger spicules may be striated on distal half. Dorsum variegated with greenish-blue and cream. Sutural tufts and marginal fringe well-developed, composed of long, straight, smooth spicules, colored light green.

Distribution: Subtidally to 20 m, from southern California to Baja California Sur and the Gulf of California to Punta Cholla, Sonora, Mexico.

Material examined: USA: CALIFORNIA: San Onofree (MCZ); La Jolla, Bird Rock; La Jolla, Devil's Slide (both DMNH); La Jolla; False Bay (both AMNH); Catalina Id.; Newport Beach; San Diego, Stearn's Cove (all USNM); San Diego (AMNH, ANSP, USNM). MEXICO: SONORA: Punta Cholla (ANSP); BAJA CALIFORNIA: Ensenada (GTW); Agua de Chale (AMNH); Bahía de Los Angeles (AJF); Bahía de Los Animas (USNM); BAJA CALIFORNIA SUR: Bahía Pichilinque (USNM).

Fossil records (unconfirmed): PLEISTOCENE: California, Santa Monica, Long Wharf Canyon, Upper San Pedro Series (BERRY, 1922).

Remarks: Uncertainty of the true status of some western acanthochitons has resulted in the misidentification of perhaps two other species for *Acanthochitona avicula*: *A. angelica* certainly has been confused with it and *A. imperatrix* may also be listed in collections as *A. avicula*. Of the three species *A. avicula* appears to be the most common and probably inhabits shallower water; it is recognized by the very elongate pustules and the coarse, bent, dorsal girdle elements.

The type of *Acanthochitona avicula* is a small specimen only 4.3 mm in length, but has the characteristic sculpture and girdle elements of the more commonly seen larger individuals. PILSBRY (1893b) introduced the variety *diegoensis* for specimens having larger girdle elements, smaller pustules, and a different posterior valve profile and added (p. 25): "This may prove to be the adult form of Carpenter's *avicula*." Although the morphological differences Pils-

bry cited cannot be shown with the available material to be ontogenetic, they do fall within the range of variation of this species. Specimens depicting a wide range of variability have been found in the same locality.

Acanthochitona imperatrix Watters, 1981

(Figures 31–39, 89)

Acanthochitona sp. ?: SMITH & FERREIRA, 1977:82, 97; fig. 22.
Acanthochitona imperatrix WATTERS, 1981b:171–173; pl. 1a–c; pl. 4b; FINET, 1985:11; LYONS, 1988b:150; SKOGLUND, 1989:87.

Type material: *Acanthochitona imperatrix* Watters, 1981. Holotype: USNM 218762. Paratypes: ANSP 153484, USNM 225346.

Type locality: U.S. Fish Commission Sta. 2824, 8 fms (14.6 m) off San Diego, California, USA, 24°22′30″N, 110°19′30″W; taken with tangles on broken shell bottom, 30 April 1888, by the U.S. Fish Commission.

Description (from WATTERS, 1981b): Holotype 8.9 mm in length, curled. Tegmentum of intermediate valves about twice as wide as long, flattened, not carinated. Beaks prominent. Jugum very wide, flat, smooth, and distinctly raised above latero-pleural areas. Jugal macresthetes widely spaced, arranged in longitudinal rows, each accompanied by 0–2 micresthetes. Latero-pleural areas sculptured with numerous teardrop-shaped, close-set pustules, each moderately elevated and concave. Each pustule bearing one centrally located macresthete. Zero to five micresthetes (commonly 0) accompanying each macresthete and generally confined to area posterior to macresthete. Mucro central and prominent with concave postmucronal slope. Tegmentum uniformly peach-colored, jugum lighter. Alternating spots of cream and maroon present along posterior borders of values and flanking jugum on holotype.

Apophyses extensive. Slit formula 5-1-2. Articulamentum cream-colored, tinged with green towards beaks.

Dorsum of girdle velvety, armed with dense, very minute spicules; spicules monomorphic, round in cross-section, smooth, and slightly bent. Girdle dorsum peach-colored, ventral side slightly darker. Marginal fringe and sutural tufts well-developed in juveniles, composed of numerous long, slender spicules.

Distribution: Subtidally to at least 17 m from lower California to the Galápagos Ids. It is not endemic to the Galápagos Ids., as indicated by FINET (1985:11).

Material examined: USA: CALIFORNIA: off San Diego, U.S. Fish Commission Sta. 2824, 24°22′30″N, 110°19′30″W (USNM). MEXICO: BAJA CALIFORNIA SUR: off La Paz, U.S. Fish Commission Sta. 2826, 24°12′00″N, 109°55′00″W (USNM). ECUADOR: GALÁPAGOS ISLANDS: Isla Santa Cruz (Indefatigable Id.), Seymour Bay (ANSP).

Remarks: This species is apparently very rare in collections, although additional examples may be misidentified

in private collections as *Acanthochitona avicula*. It can be recognized by the wide, flat, smooth, distinctly raised jugum. The girdle elements are much finer than those of *A. avicula*. It is not closely related to other New World species and is placed in the *A. angelica*-complex with reservation. It most closely resembles *A. mahensis* Winckworth, 1927, from Mahé, Madras, India, and *A. bisulcatus* Pilsbry, 1893, from an unknown locality.

Acanthochitona hirudiniformis complex

These species are generally large, characterized by pentagonal valves, as wide as long, a low, posteriorly acentric mucro, and sculpturing with numerous small, round to oval pustules. The jugum may be smooth or striated. The dorsum of the girdle is generally covered with fine, velvety spicules; the sutural tufts are composed of many very fine spicules. In addition to *Acanthochitona hirudiniformis*, the complex contains the Caribbean *A. astriger* (Reeve, 1847), *A. lineata* Lyons, 1988, and *A. worsfoldi* Lyons, 1988, the west African *A. garnoti* (de Blainville, 1825), and the Hawaiian *A. viridis* (Pease, 1872), among others, as well as the fossil species *Acanthochitona plana* and *Acanthochitona* sp. I, both of ŠULC (1934).

Placed here with some reservation are a small group of Acanthochitoninae with marked *Notoplax*-like features. They may represent an extreme expression of the *Acanthochitona hirudiniformis* complex, or possibly constitute a separate genus or subgenus of *Acanthochitona*. The group includes the Caribbean *A. hemphilli* (Pilsbry, 1893) and *A. rhodea* (Pilsbry, 1893), the eastern Pacific *A. ferreirai* Lyons, 1988, and *A. mastalleri* Strack, 1989, from the Red Sea, and probably *Notoplax eximia* Thiele, 1909, from Sulawesi.

Acanthochitona hirudiniformis hirudiniformis
(Sowerby I, 1832)

(Figures 40–50, 53–59, 92)

Chiton hirudiniformis SOWERBY I (in Broderip & Sowerby I), 1832:59; SOWERBY II, 1840:7; figs. 23, 142; ADAMS, 1847:25; D'ORBIGNY, 1847:484.
Chiton hirudinifomis [sic] Sowerby I: REEVE, 1847:pl. 10, fig. 54.
Phakellopleura (Acanthochites) hirundiniformis [sic] (Sowerby I): SHUTTLEWORTH, 1853:206, 207.
Acanthochites hirudiniformis (Sowerby I, 1832): WIMMER, 1879:506; STEARNS, 1893:410; PILSBRY, 1893b:27; pl. 2, figs. 49, 56; PILSBRY & VANATTA, 1902:552; NIERSTRASZ, 1905:61; THIELE, 1908:17; DALL, 1909:246; THIELE, 1909:4.
Acanthochiton hirudiniformis (Sowerby I): HADDON, 1886:35, 36; THIELE, 1893:398; pl. 32, fig. 30; LELOUP, 1941:1; LELOUP, 1956:5, 27–29, 86, 88, 89, 92; fig. 8.
"?Tonicia hirudiniformis (Sowerby)": STEARNS, 1893:449.
Chiton (Acanthochites) hirudiniformis Sowerby I: CLESSIN, 1904:59; pl. 22, fig. 2.
Chiton hyrundiniformis [sic] Sowerby I: CLESSIN, 1904:59.
Chiton (Acanthochites) hirudiformis [sic] Sowerby I: CLESSIN, 1904:59.
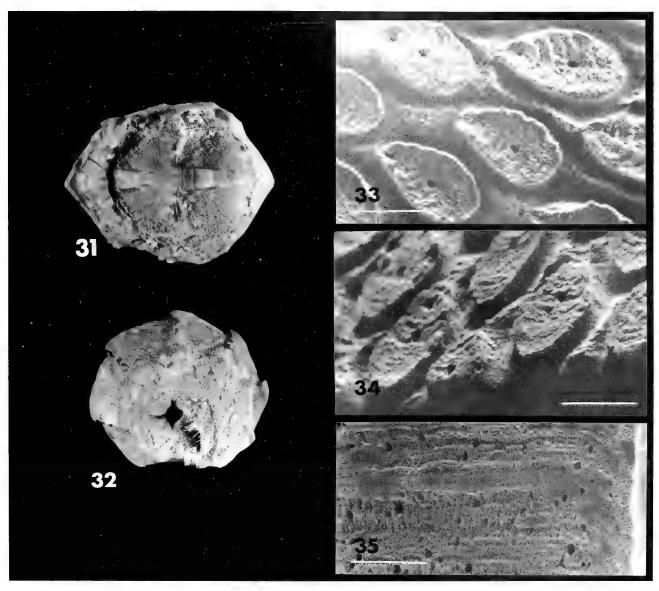
Explanation of Figures 31 to 35

Figures 31–35. *Acanthochitona imperatrix* Watters, 1981.

Figures 31, 32. Holotype of *Acanthochitona imperatrix* Watters, 1981, San Diego, California, USA (USNM) (8.9 mm, greatest dimension of curled individual).

Figures 33–35. Paratype of *Acanthochitona imperatrix* Watters, 1981, San Diego, California, USA (USNM).

Figure 33. Dorsal view of pustules (scale = 100 μm).

Figure 34. Oblique view of pustules (scale = 100 μm).

Figure 35. Dorsal view of jugum (scale = 100 μm).

Acanthochitona hirundiniformis [*sic*] (Sowerby I): DALL, 1919: 515; FINET, 1985:11.
Acanthochitona hirudiniformis (Sowerby I): HERTLEIN, 1963: 242; THORPE, 1971:866, 868; fig. 13; SMITH & FERREIRA, 1977:82, 92, 93, 95; fig. 17; KAAS & VAN BELLE, 1980: 60; WATTERS, 1981a:77; LYONS, 1988a:87, 91, 92, 98, 112, 113; figs. 52–56; SKOGLUND, 1989:87.
Acanthochitona hirudiniformis hirudiniformis (Sowerby I): WATTERS, 1981b:173.
Acanthochitona panamensis "Pils.": PILSBRY & LOWE, 1932: 130 [*nomen nudum*]; KAAS & VAN BELLE, 1980:95.

Acanthochiton coquimboensis LELOUP, 1941:1–4; fig. 1; pl. 1, fig. 1; KAAS & VAN BELLE, 1980:31.

Acanthochitona coquimboensis (Leloup): THORPE, 1971:866; SMITH & FERREIRA, 1977:93; KAAS & VAN BELLE, 1980: 31; WATTERS, 1981b:173.

Acanthochitona tabogensis A. G. SMITH, 1961:87; pl. 9, fig. 1 [new name for *A. panamensis* Pilsbry & Lowe, 1932]; THORPE, 1971:886; SMITH & FERREIRA, 1977:93; KAAS & VAN BELLE, 1980:129; WATTERS, 1981b:173; LYONS, 1988a:82.

Figure 36

Distribution of *Acanthochitona imperatrix* Watters, 1981.

"*Chiton (Radsia) stokesii,*" BIOLLEY, 1907:24 [*non* Broderip, 1832, *fide* HERTLEIN, 1963:242].

Non *Acanthochites hirudiniformis* "Pilsbry," DUNKER, 1882: 160 [?=*Acanthochitona rubrolineata* (Lischke, 1873)].

Non *Acanthochiton hirudiniformis* "Sowerby," STUARDO, 1959: 143, 145 [=*Acanthochitona hirudiniformis peruviana* (Leloup, 1941)].
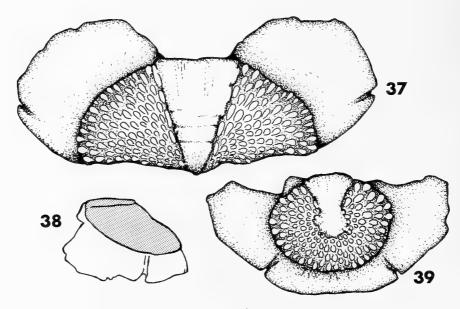
Type material: *Chiton hirudiniformis* Sowerby I, 1832. Syntypes: BMNH 1984050.

Acanthochiton coquimboensis Leloup, 1941. Syntypes: BMNH 1886.6.9.705; originally three specimens, the illustrated specimen (pl. 1, fig. B) cannot be located (*in litt.,* S. Morris, 21 March 1989). Type locality: Coquimbo, Peru.

Acanthochitona tabogensis A. G. Smith, 1961. Holotype: SDMNH 23666. Type locality: Taboga Id., western Panama.

Type locality: "*ad littora Peruviae* (Ançon, Lobos Island, and Payta), *et ad insulis Gallapagos* (Chatham Island)," restricted by SMITH & FERREIRA (1977) to Chatham Id. (Isla San Cristobal), Galápagos Ids., Ecuador; restored here to Sowerby's original type locality (see below).

Description: Largest specimen seen, 36 mm in length, strongly curled. Tegmentum of intermediate valves about as wide as long, pentagonal in outline. Beaks not prominent. Jugum smooth except for growth lines in northern populations, but longitudinal striations may occur in south. Some southerly individuals may alternate between striated and non-striated jugal sculpture. Jugal macresthetes arranged in irregular longitudinal rows, each accompanied by 3–6 microsthetes. Latero-pleural areas sculptured with numerous oval or teardrop-shaped pustules, each pustule bearing one centrally located macresthete and 0–4 micresthetes confined to premacresthete area. Mucro central, not prominent, postmucronal slope straight or convex. Tegmentum uniformly colored dark greenish-brown, many mainland specimens with paler bands parallel to jugum.
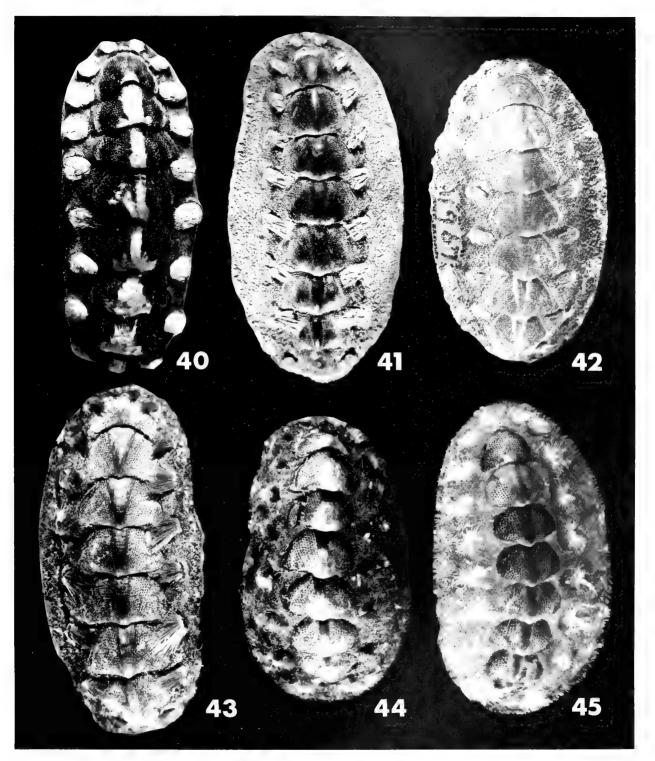
Explanation of Figures 37 to 39

Figures 37–39. Paratype of *Acanthochitona imperatrix* Watters, 1981, San Diego, California, USA (USNM).

Figure 37. Intermediate valve VII? (3.9 mm width).

Figure 38. Posterior valve profile.

Figure 39. Posterior valve (2.8 mm width).

Explanation of Figures 40 to 45

Figures 40–45. *Acanthochitona hirudiniformis hirudiniformis* (Sowerby I, 1832).

Figure 40. Syntype of *Acanthochiton coquimboensis* Leloup, 1941 (BMNH) (16.9 mm).
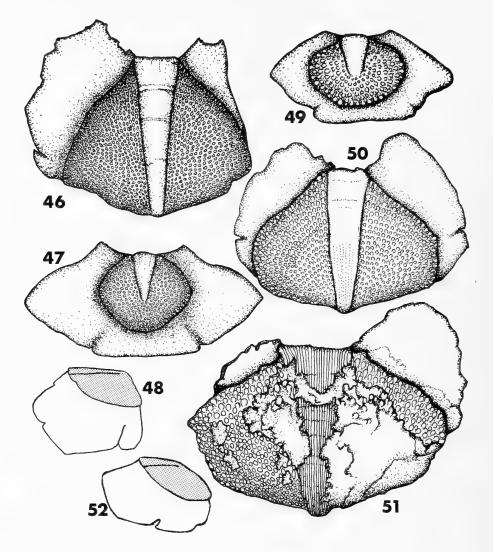
Figure 41. Syntype of *Chiton hirudiniformis* Sowerby I, 1832 (BMNH) (26.5 mm).

Figure 42. Holotype of *Acanthochitona tabogensis* A. G. Smith, 1961, Taboga Id., Panama (SDMNH) (30 mm).

Figure 43. Isla Pinzón (Duncan Id.), Galápagos Ids., Ecuador (GTW) (20 mm).

Figure 44. Flamenco Id., Canal Zone (RCB) (20 mm).

Figure 45. Flamenco Id., Canal Zone (RCB) (25 mm).

Explanation of Figures 46 to 52

Figures 46–48. *Acanthochitona hirudiniformis* (Sowerby I, 1832), Isla Pinzón, Galápagos Ids., Ecuador (GTW).

Figure 46. Intermediate valve VII (6 mm width).

Figure 47. Posterior valve (6 mm width).

Figure 48. Posterior valve profile.

Figures 49–50. *Acanthochitona hirudiniformis* (Sowerby I, 1832), San Juan del Sur, Nicaragua (SDMNH).

Figure 49. Posterior valve (4 mm width).

Figure 50. Intermediate valve V (5.5 mm width).

Figures 51, 52. *Acanthochitona hirudiniformis peruviana* (Leloup, 1941), Valparaiso, Chile (USNM).

Figure 51. Intermediate valve VII (3.9 mm width).

Figure 52. Posterior valve profile.

Apophyses well-developed. Slit formula 5-1-2. Articulamentum flushed with green, brownish towards beaks.

Girdle dorsum densely covered with needlelike spicules. In northern part of range, dorsal elements monomorphic, smooth, and slightly bent; in southern populations, larger, stouter, straight element may be found interspersed among smaller elements characteristic of north. New element may or may not be striated. Girdle dark green in color. Sutural tufts and marginal fringe may be well-developed; bronze in color. Worn specimens may be devoid of spicules.

Distribution: Intertidally to at least 2 m from the Gulf of California through western Central America to Peru and the Galápagos Ids. Lyons (1988a:92) states that this species occurs "intertidally on high energy rocky shores."

Material examined: Mexico: Baja California: Bahía Las Animas (USNM). Nicaragua: Puerto San Juan del Sur (ANSP). Costa Rica: Bahía Huevos (ANSP); Bahía Cocos (DMNH). Panama: Tonosi Búcaru (AMNH); Isla Tobago (ANSP, SDMNH); Punta Patilla (GTW); Cam-

eron (AMNH); Punta Mala (RCB); Naos Id.; Punta del Toro; Pearl Id. (all USNM). CANAL ZONE: Flamenco Id.; Culebra Id. (both RCB). PERU: (AMNH, ANSP); Payta (MCZ). ECUADOR: GALÁPAGOS ISLANDS: Isla Fernandina (Narborough Id.); Isla Isabella (Albemarle Id.), Tagus Cove (both ANSP); Isla San Salvador (James Id.) (MCZ); Isla Pinzón (Duncan Id.) (ANSP, DMNH, GTW); Isla Santa Cruz (Indefatigable Id.), Bahía de la Academía (AMNH, DMNH, GTW, USNM); Isla Santa Fé (Barrington Id.) (AMNH); Isla Santa María (Charles Id.) (MCZ).

Fossil records: None reported.

Remarks: SOWERBY I (1832) based his description of *Acanthochitona hirudiniformis* on a series of specimens from Ançon, Lobos Id., and Payta (all Peru) and Chatham Id., Galápagos Ids., Ecuador. The variation of this species and the broad range of Sowerby's type locality has caused subsequent workers to puzzle over exactly how many taxa were included in Sowerby's syntype lot, and which one(s) actually represented *A. hirudiniformis*. LELOUP (1941), working with a very small sample of Peruvian specimens, described two new species: *A. peruviana* and *A. coquimboensis*. Neither was compared with *A. hirudiniformis*, though Leloup did state that *A. coquimboensis* differed from it "sous tous rapports" (p. 1). THORPE (1971) synonymized Leloup's two species with *A. hirudiniformis* but gave no reason for this action. SMITH & FERREIRA (1977) questioned Thorpe's conclusions and suspected that several taxa were involved; they believed that consistent differences appeared to exist between Galápagos and mainland populations, particularly in the size of the pustules and the morphology of the girdle elements. For this reason they restricted the type locality of *A. hirudiniformis* to Chatham Id., as suggested by Pilsbry in manuscript. They suggested that the mainland forms, if indeed different, may be allocated to one (or both) of Leloup's names or to Smith's *A. tabogensis* (1961), described from the Bay of Panama. This was an unfortunate action for the following reasons. The syntype lot contains specimens from four different localities, but there is no indication of which specimen is from which locality. SMITH & FERREIRA (1977) restricted the type locality but did not select a lectotype; in fact they could not select one. Thus a situation was created in which the type locality could not be paired with any specimen of the syntype lot. Conversely, I cannot designate a lectotype corresponding to the Ecuadorian locality. ICZN rules do not address this issue. I feel that it is best to reject Smith and Ferreira's type locality restriction and to restore the type locality to Sowerby's original broad range. For these same reasons, I have not designated a lectotype for this species.

PILSBRY & LOWE (1932:130), in a list of mollusks from west Mexico and Central America, recorded "*Acanthochitona panamensis* Pils. Under stones at extreme low tide, quite rare. Taboga Island; Montijo Bay; San Juan del Sur." This name was never officially introduced and is a
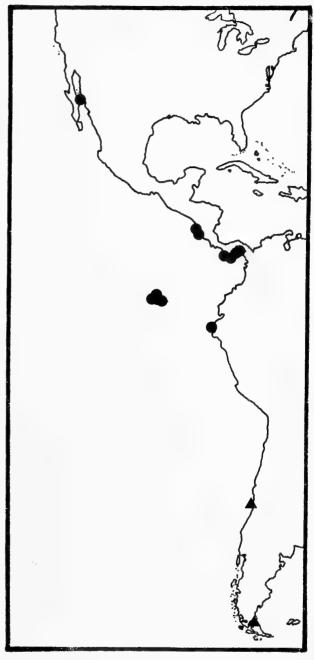
Figure 53
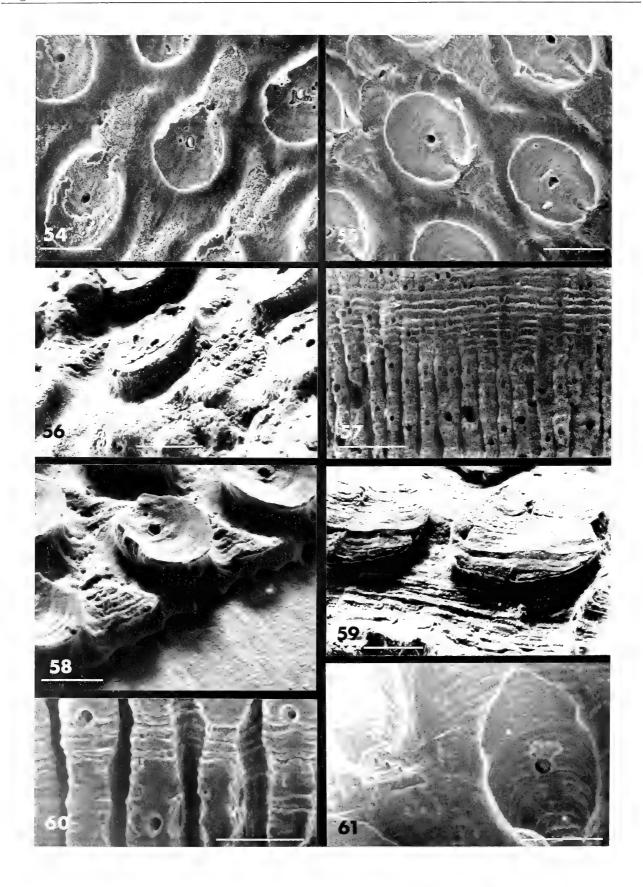
Distribution of *Acanthochitona h. hirudiniformis* (Sowerby I, 1832) (●) and *Acanthochitona h. peruviana* (Leloup, 1941) (▲).

nomen nudum. A. G. SMITH (1961), working with Pilsbry's proposed type of *A. panamensis* (ANSP 153556), and additional material from Nicaragua, introduced this species under the name *A. tabogensis* from Taboga Island. However, additional lots of "*A. tabogensis*" (SDMNH 23659), identified as such by Smith, are examples of *A. ferreirai*.

In addition to *Acanthochitona coquimboensis*, *A. peruvi-*

anus, A. panamensis, and *A. tabogensis,* two other names (both *nomen nuda*) were proposed for local variants of *A. hirudiniformis,* and exist in collections, but were never introduced. Examination of the material at the Museum of Comparative Zoology yielded "*Acanthochiton hassleri* Cpr. type" from Payta, Peru, collected by the Hassler Expedition (MCZ 1260 and another unnumbered lot). The Academy of Natural Sciences collection contains a lot, ANSP 35788, of one whole and one broken, disarticulated specimen of a very large acanthochiton (36 mm in length, strongly curled) labeled as type and paratype of "*A. inca* Pilsbry MS" from Peru (*non Chiton inca* d'Orbigny, 1841, or von Wissel, 1904). SMITH & FERREIRA (1977) stated that the ANSP specimens were purchased in London between 1846 and 1849, probably from Hugh Cuming. Both "*A. hassleri*" and "*A. inca*" differ from Galápagos and Central American specimens primarily in possessing large, stout, dorsal girdle elements among the finer, more numerous elements typical of northern populations.

Acanthochitona hirudiniformis extends along the coast of the western New World from Baja California to Tierra del Fuego in a narrow longitudinal range. Although breeding theoretically can occur between members throughout the entire range, it is far less likely that northern and southern individuals interbreed than do contiguous segments of the population. The results may be a north-to-south cline in characteristics, in particular girdle element composition and jugal sculpture. Northern populations possess only needlelike dorsal elements, while in Peru stout, blunt spicules appear occasionally among them. From Chile south the stout elements appear almost exclusively of the needlelike spicules. Northern populations have a smooth jugum while southern individuals have only striated jugums; Peruvian examples may have both striated and nonstriated jugal regions on the same individual (Figure 57). Although specimens south of Peru are extremely rare in collections, the few available seem to be homogeneous in their characteristics. The regions north and south of Peru may be interpreted as a pronounced clinal step and the two populations considered as subspecies (MAYR, 1969): *A. h. hirudiniformis* in the north and *A. h. peruviana* in the south. I cannot find sufficient differences to warrant the

separation of the Galápagos Ids. population from the mainland individuals. The variability of this species throughout its range has resulted in the several aforementioned names applied to local variants; only two subspecies are recognized here. They may have arisen as the result of the South Equatorial Current, which originates off the coast of Peru, dividing the western coast of South America in two at that point. BULLOCK (1988) found that *Chiton magnificus* Deshayes, 1827, was also divided into north and south subspecies along western South America, although not at this point.

Acanthochitona h. hirudiniformis, particularly Peruvian specimens, may be confused with *A. h. peruviana.* Although the Peruvian examples of the former may possess the stout girdle elements of *A. h. peruviana,* the predominant elements on the dorsum are the slender, needlelike spicules of the more northern specimens. This species is most similar to several Caribbean taxa: *A. astriger* (Reeve, 1847), which possesses slightly finer and straighter dorsal elements, *A. worsfoldi* Lyons, 1988, a much smaller species with very fine dorsal elements and fewer sutural tuft spicules, and *A. lineata* Lyons, 1988, which has relatively larger tegmental pustules and longer dorsal elements.

Acanthochitona hirudiniformis peruviana
(Leloup, 1941)

(Figures 51–53, 60, 61)

Acanthochiton peruviana LELOUP, 1941:6–9; figs. 4, 5; pl. 1, fig. 3; KAAS & VAN BELLE, 1980:99.
Acanthochiton peruviana (Leloup): THORPE, 1971:866.
Acanthochitona hirudiniformis peruviana (Leloup): WATTERS, 1981b:173.
Acanthochiton hirudiniformis "Sowerby": STUARDO, 1959:143, 145.
Acanthochitona sp.: SMITH & FERREIRA, 1977:93.

Type material: *Acanthochiton peruviana* Leloup, 1941. Holotype: Musée royal d'Histoire naturelle de Belgique.

Type locality: "Perou."

Description: Largest specimen, 23 mm in length. Tegmentum of intermediate valves pentagonal in outline, flat-

←

Explanation of Figures 54 to 61

Figures 54–59. *Acanthochitona hirudiniformis hirudiniformis* (Sowerby I, 1832).

Figure 54. Dorsal view of pustules, Cameron, Panama (AMNH) (scale = 100 μm).

Figure 55. Dorsal view of pustules, Punta Patillo, Panama (GTW) (scale = 100 μm).

Figure 56. Oblique view of pustules, Cameron, Panama (AMNH) (scale = 100 μm).

Figure 57. Dorsal view of jugum, Cameron, Panama (AMNH) (scale = 100 μm).

Figure 58. Oblique view of pustules, Punta Patillo, Panama (GTW) (scale = 100 μm).

Figure 59. Oblique view of pustules, "Peru" (ANSP) (scale = 100 μm).

Figures 60, 61. *Acanthochitona hirudiniformis peruviana* (Leloup, 1941), Valparaiso, Chile (USNM).

Figure 60. Dorsal view of jugum (scale = 100 μm).

Figure 61. Dorsal view of pustules (scale = 100 μm).

tened, not carinated. Beaks prominent. Jugum cut by numerous (ca. 20) finely incised, longitudinal striations that appear granulose. Jugal macresthetes arranged in single rows per striation, with no accompanying micresthetes. Latero-pleural areas finely pustulose, pustules oval to teardrop-shaped. Each pustule bearing one centrally located macresthete with 2–6 micresthetes distributed on pustule or confined to prepustular slope. Mucro posteriorly acentric, fairly prominent, post-mucronal slope convex. Tegmentum uniformly white, greenish-brown, or brown, with scattered flecks of lighter shades. Jugum may be darker in color and paralleled by lighter band on each side.

Apophyses moderately extensive. Slit formula 5-1-2. Articulamentum white, tinged with rose towards beaks.

Girdle dorsum covered with large, coarse, striated spicules between which may be much smaller, smoother elements. Girdle greenish-gray or greenish-brown; coarse elements with tan or dark green tips. Sutural tufts and marginal fringe not complete in known examples but appear to be composed of numerous, needlelike spicules.

Distribution: The records of the few known specimens indicate a patchy distribution from Peru to Tierra del Fuego; nothing is known of this bathymetric range. With the exception of *Acanthochitona fascicularis*, which may have been fortuitously introduced to Tierra del Fuego (USNM; BMNH), and *Notoplax magellanica* Thiele, 1909, which I have not seen, this is the most southern species of the family in the New World.

Material examined: CHILE: Valparaiso; Tierra del Fuego, Orange Harbour (both USNM).

Remarks: LELOUP (1941) described this species based upon a single specimen in the Musée royal d'Histoire naturelle de Belgique labeled "*Chiton limaciformis* Sow. Perou, coll. Haas." I have located two additional specimens of this rare species in the U.S. National Museum of Natural History, both very poorly preserved.

The better preserved of the two (USNM 5804) is an entire, curled individual that at some time had been glued to a card or box. Much of the girdle has been worn away so that the only intact section of the girdle is the part that had been covered with glue. A series of labels accompany the specimen. The first bears the inscription "5804 *Acanthochiton*" on a U.S. Exploring Expedition label annotated "Orange Harbor, Patagonia, South America." A second label reads: "*Acanthochiton* sp. ind. The specimen sent in the box was *Phakellopleura violacea*." On the same label in different ink is the notation "Orange Har.? Sent as the type of *Ch. viridulus* Gld.—Pl. 27, f. 413 but does not resemble the specimen figured" and is signed with Carpenter's initials. A third label reads "5804 *Acanthochites hirudiniformis* Sby. Orange Harbor, Patagonia, U.S. Ex. Exp." The coloration of the specimen and the naked girdle could result in the misidentification of this individual for *Phakellopleura violacea* [=*Notoplax violaceus* (Quoy & Gaimard, 1835)]. I suspect that the specimen was sent labeled

as *Chiton viridulus* [=*Ischnochiton viridulus* (Gould, 1846)]. Carpenter, upon finding the specimen to be in disagreement with published figures, reidentified it (erroneously) as *P. violaceae*. At some subsequent time it was again reidentified as *A. hirudiniformis*.

The second specimen (USNM 19284) from Valparaiso, also collected by the U.S. Exploring Expedition, is disarticulated with the valves broken, weathered, and bleached. The girdle is nearly devoid of spicules. It was identified as *A. "hirundiniformis"* [*sic*] by Carpenter.

SMITH & FERREIRA (1977:93) discussed both of these specimens under the "remarks" section of *Acanthochitona hirudiniformis*. They concluded that these chitons "probably represent other species." THORPE (1971) placed *A. peruviana* in synonymy with *A. hirudiniformis* without presenting evidence for this conclusion.

Acanthochitona h. peruviana represents one of the rarest species of New World acanthochitons in collections. Its rarity, however, is probably not due to the inaccessibility of the western South American-Patagonian region for collecting, as numerous reports on the Chilean-Magellanic chitons have been published that make no mention of an acanthochiton: FREMBLY, 1827; THIELE, 1906, 1911; MELVILL & STANDEN, 1912; BERGENHAYN, 1937; LELOUP, 1937, 1956, 1980; CASTELLANOS, 1948, 1951, 1956; BARATTINI, 1951; CARCELLES, 1950, 1953; CARCELLES & WILLIAMSON, 1951; STUARDO, 1959, 1964. Other accounts report *A. stygma* and *A. conthouyi*, both de Rochebrune, 1889. I believe *A. stygma* to be the leptochitonid *Hemiarthrum setulosum* Dall, 1876, and KAAS & VAN BELLE (1980, 1985) believe *A. couthouyi* also to be that species.

Acanthochitona ferreirai Lyons, 1988

(Figures 62–66)

> *Acanthochitona rhodea* KEEN, 1958:519; fig. 10 [in part]; A. G. SMITH, 1961:89; THORPE, 1971:867, 868; fig. 14; BULLOCK, 1974:164 [in part]; FERREIRA, 1985:207, 208 [in part] [*non* Pilsbry, 1893].
> *Acanthochitona ferreirai* LYONS, 1988a:79, 85, 86, 112, 113; figs. 19–24; SKOGLUND, 1989:87.
> ?*Acanthochites rhodeus* Pilsbry: NIERSTRASZ, 1905:60.

Type material: *Acanthochitona ferreirai* Lyons, 1988. Holotype: USNM 859314; no paratypes were available for study.

Type locality: Punta Mala, [western] Panama.

Description (from LYONS, 1988a:85, 86): Largest specimen (holotype), 28.2 mm long, 17.0 mm wide, including girdle; valves occupying approximately 65% of total specimen width. Exposed valves uniformly red or rose, usually with white maculations; unexposed parts rose pink. Girdle broad, orange-brown or dark red, with large white patches of spicules unevenly spread across dorsal surface; spicules of dorsal tufts green.

Valve i semilunate, wider than long, concave posteriorly, with anterior insertion plate bearing 5 slits; tegmentum

Explanation of Figures 62 and 63

Figures 62, 63. *Acanthochitona ferreirai* Lyons, 1988.

Figure 62. Holotype of *Acanthochitona ferreirai* Lyons, 1988, Punta Mala, Panama (USNM) (28.2 mm).
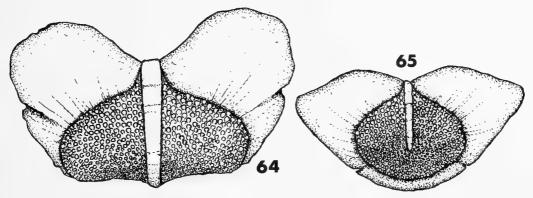
Figure 63. San Juan del Sur, Nicaragua (SDMNH) (25 mm).

occupying about 65% total valve length. Valves ii–vii beaked; tegmentum alate, twice as wide as long, constricted anteriorly, with anteriolateral margins concave near jugum; sutural laminae broad, flared anterolaterally, separated anteriorly by wide, shallow sinus; lateral areas near midpoints of margins. Valve viii broadly triangular, twice as wide as long, rounded posteriorly, with nearly central mucro; tegmentum ovate, wider than long, constricted anteriorly along jugum; sutural laminae very wide, flared anterolaterally, with straight anterior margins, separated by very shallow, broad, V-shaped sinus; 2 slits in posterior insertion plate small, narrow, V-shaped.

Jugum smooth, narrow, with parallel sides well-separated from lateral tegmentum surface, extended anteriorly beyond main tegmentum mass. Tegmentum of all valves covered with small (100 μm) round to slightly ovate pustules, with subcentral macresthete, 3–4 micresthetes.

Girdle upper surface covered with dense mat of very small (60 μm) spicules overlain by extensive patches of slender, straight, white spicules 400–500 μm long, especially evident posteriorly and where girdle intrudes between valves; 18 anterior and sutural tufts containing 50–60 straight or slightly curved, stout, sharp-tipped green spicules up to 2.2 mm long; margin fringed with slender, sharp-tipped spicules up to 1 mm long, arranged in alternating groups of purple and white; underside densely covered with slender, sharp-tipped spicules about 80–90 μm long, directed toward periphery.

Distribution: LYONS (1988a:85) gave the distribution as the "Pacific coasts of Costa Rica and Panama; intertidal and shallow subtidal depths." It apparently extends north as far as Sonora, Mexico; records from Peru have not been substantiated.

Explanation of Figures 64 and 65

Figures 64, 65. *Acanthochitona ferreirai* Lyons, 1988, Punta Mala, Panama (FSBC). Redrawn from LYONS (1988a).

Figure 64. Intermediate valve IV (ca. 23 mm).

Figure 65. Posterior valve (ca. 11 mm).

valves, and the leathery aspect of the girdle separate this from sympatric species. Only *Acanthochitona exquisita* also possesses a high degree of girdle encroachment, but that species has an olive-green girdle and tegmentum and enormously produced sutural tufts. From the original description, *Notoplax eximia* Thiele, 1909, from Cape Rivers, Celebes (=Sulawesi), appears to be extremely close to this New World group.

Acanthochitona exquisita (Pilsbry, 1893)

(Figures 67–76, 93)

Acanthochites exquisitus PILSBRY, 1893a:32; PILSBRY, 1893b: 23; pl. 12, figs. 44–47; PILSBRY, 1893c:95, 96; NIERSTRASZ, 1905:60.
Acanthochitona exquisita (Pilsbry): DALL, 1919:515; PILSBRY & LOWE, 1932:130; LOWE, 1933:112; STEINBECK & RICKETTS, 1941:220, 549, 551, 556; pl. 27, fig. 1; M. SMITH, 1944:70; KEEN, 1958:519; fig. 9; McLEAN, 1961: 453, 454, 456, 473; DUSHANE, 1962:50; PARKER, 1964: 151, 166; COAN, 1968:130; DUSHANE & SPHON, 1968: 235, 244; THORPE, 1971:866; fig. 12; DANCE, 1973:42, 43; fig. 3; HOUSTON, 1973:178; fig. 6.75; ABBOTT, 1974: 407; HOUSTON, 1980:195; fig. 9.229; KAAS & VAN BELLE, 1980:45; WATTERS, 1981b:173; ABBOTT & DANCE, 1982: 287; 1 fig.; SKOGLUND, 1989:87.
Acanthochiton exquisitus (Pilsbry): LELOUP, 1941:4–6; figs. 2, 3; pl. 1, fig. 2; FISCHER, 1978:37.
Acanthochites exquisitus variety *ampullaceus* PILSBRY, 1893b: 24; pl. 4, fig. 85; NIERSTRASZ, 1905:60.
Acanthochiton exquisitus variety *ampullaceus* (Pilsbry): LELOUP, 1941:6.
Acanthochitona exquisita ampullacea (Pilsbry): KAAS & VAN BELLE, 1980:45.
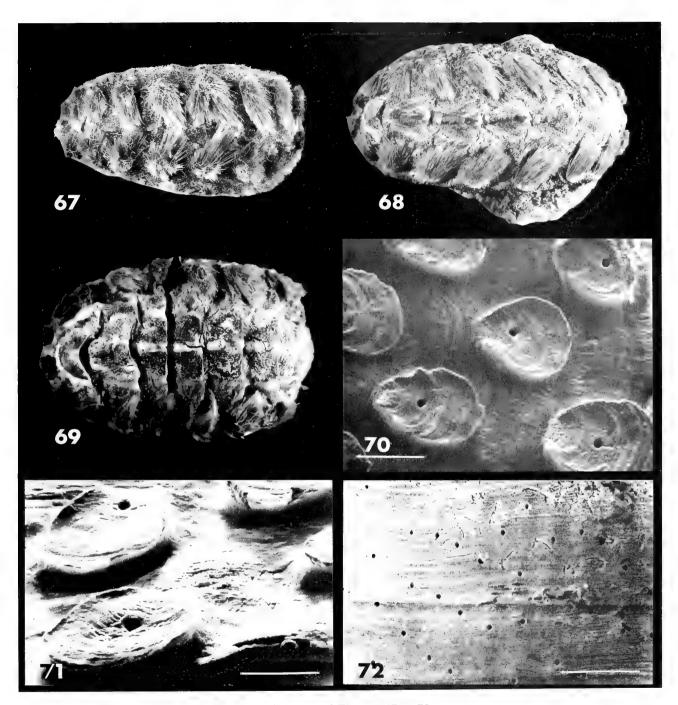
Type material: *Acanthochites exquisitus* Pilsbry, 1893. Lectotype: herein designated (ANSP 349332).
Acanthochites exquisitus variety *ampullaceus* Pilsbry, 1893. Lectotype: herein designated (ANSP 349329). Type locality: La Paz (Baja California Sur, Mexico).

Type locality: Las Animas Bay, Baja California, Mexico. In the original description of *Acanthochitona exquisita*, PILSBRY (1983a) gave the type locality as La Paz (Baja California Sur, Mexico), but later (1893c) stated that that information was in error and corrected the type locality to Las Animas Bay (in accordance with ICZN Art. 72H (b)). This correction has been overlooked by other workers. The type locality of the syntype lot of *A. e. ampullaceus* was also given as La Paz but PILSBRY did not mention in his 1893c paper whether this type locality designation was also erroneous. It is possible that Pilsbry extracted the syntypes of *A. e. ampullaceus* from a series of *A. exquisita* from Las Animas, but in lieu of more information, the type locality of *A. e. ampullaceus* must stand as La Paz.

Description: Largest specimen, 47 mm in length. Tegmentum of intermediate valves much longer than wide, triangular, very reduced relative to the articulamentum.

Figure 66

Distribution of *Acanthochitona ferreirai* Lyons, 1988.

Material examined: MEXICO: SONORA: Guaymas (AJF). NICARAGUA: San Juan del Sur (SDMNH). COSTA RICA: Puerto Quepos; Playa de Jaco, Puntarenas (both AJF). PANAMA: Punta Mala (RCB, USNM). CANAL ZONE: Flamenco Id. (RCB).

Remarks: This species, and its congeners *Acanthochitona rhodea* and *A. hemphilli*, both of PILSBRY, 1893, have been the subject of considerable confusion. Historically, *A. hemphilli* has been considered the Caribbean species and *A. rhodea* the eastern Pacific taxon, without much evidence to support this contention. In 1980 I considered (unpublished M.S. Thesis) the two to be conspecific (including the third, then undescribed species, *A. ferreirai*); I was followed in this decision by FERREIRA (1985). LYONS (1988a) has determined that *A. rhodea* and *A. hemphilli* are good species and are confined to the western Atlantic; he described the remaining eastern Pacific taxon, *A. ferreirai*, as new. I doubt that these taxa are distinct, but in lieu of more material from the eastern Pacific, I retain *A. ferreirai* as a valid species.

Acanthochitona rhodea and *A. hemphilli* were not originally described by Pilsbry in the 15th volume of the *Manual of Conchology* in 1893 as stated by KAAS & VAN BELLE (1980) and LYONS (1988a). That section was issued 16 November 1893 (*fide* VANATTA, 1927, and BOSS *et al.*, 1968); both species were described by Pilsbry in the July (possibly August) number of *The Nautilus* earlier that same year (CLENCH & TURNER, 1962).

This large chiton cannot be confused with any other eastern Pacific species; the brick-red color of the tegmentum and girdle, the encroachment of the girdle on the

Explanation of Figures 67 to 72

Figures 67–72. *Acanthochitona exquisita* (Pilsbry, 1893).

Figure 67. Puertocitos, Baja California, Mexico (GTW) (27 mm).

Figure 68. Lectotype of *Acanthochites exquisitus* Pilsbry, 1893, Las Animas Bay, Baja California, Mexico (ANSP) (29 mm).
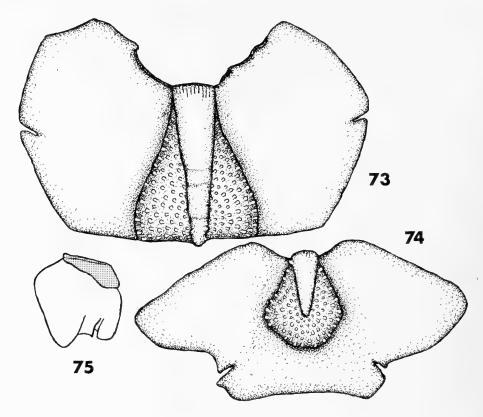
Figure 69. Lectotype of *Acanthochites exquisitus* variety *ampullaceus* Pilsbry, 1893, La Paz, Baja California, Mexico (ANSP) (20 mm).

Figures 70, 72. *Acanthochitona exquisita* (Pilsbry, 1893), Bay of Panama, Panama (GTW).

Figure 70. Dorsal view of pustules (scale = 100 μm).

Figure 71. Oblique view of pustules (scale = 100 μm).

Figure 72. Dorsal view of jugum (scale = 100 μm).

Explanation of Figures 73 to 75

Figures 73–75. *Acanthochitona exquisita* (Pilsbry, 1893), Puertocitos, Baja California, Mexico (GTW).

Figure 73. Intermediate valve VII (8.2 mm width).

Figure 74. Posterior valve (6.3 mm width).

Figure 75. Posterior valve profile.

Beaks not prominent, posterior border of intermediate valves nearly straight. Jugum smooth, very narrow, sides nearly parallel. Jugal macresthetes arranged in longitudinal rows, each accompanied by 0–3 micresthetes. Latero-pleural areas sculptured with numerous broad, teardrop-shaped pustules. Each pustule bearing one slightly posteriorly acentric macresthete with no micresthetes. Mucro posteriorly acentric, prominent, postmucronal slope slightly concave. Tegmentum uniformly dark greenish-brown.

Apophyses very extensive. Slit formula 5-1-2. Articulamentum white with flushes of green or blue towards beak.

Girdle dorsum densely covered with numerous smooth, straight needlelike spicules. Dorsum colored dark olive-green. Sutural tufts enormous, consisting of numerous very long, needlelike spicules that may conceal the tegmentum and most of girdle. Tufts and marginal fringe colored bronze, yellow, or dark translucent green.

An exceptional specimen from Las Animas Bay (USNM 58830) has tegmentum and sutural tufts colored golden-orange with white girdle, probably representing an albinistic specimen.
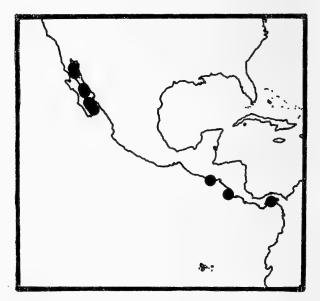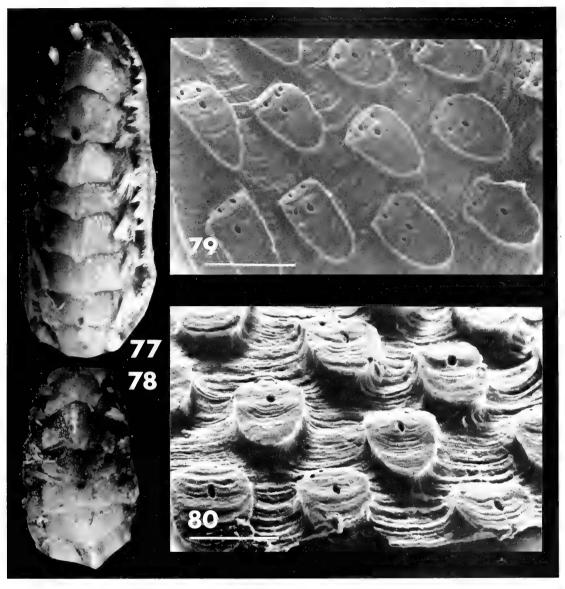
Figure 76

Distribution of *Acanthochitona exquisita* (Pilsbry, 1893).

Explanation of Figures 77 to 80

Figures 77–80. **Americhiton** *arragonites* (Carpenter, 1857).

Figure 77. Salinas, Ecuador (GTW) (4 mm).
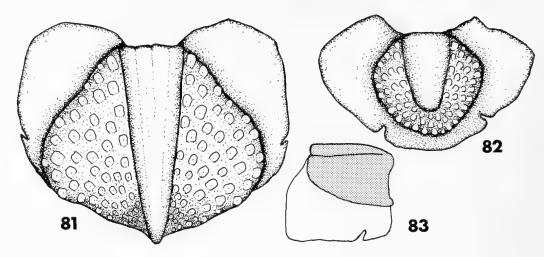
Figure 78. Lectotype of *Acanthochites arragonites* Carpenter, 1857, Mazatlán, Sinaloa, Mexico (BMNH) (3 mm).

Figures 78, 79. Bahía Kino, Sonora, Mexico (GTW) (10 mm).

Figure 78. Dorsal view of pustules (scale = 100 μm).

Figure 79. Oblique view of pustules (scale = 100 μm).

Material examined: MEXICO: BAJA CALIFORNIA: Bahía Las Animas (USNM); Bahía de Los Angeles (AMNH, MCZ); Puerto Refugio (USNM); Isla Angel de La Guarda (AMNH); Bahía San Luis Gonzaga (AMNH, DMNH, USNM); Puertocitos (AMNH, DMNH, GTW, MCZ); Agua de Chale (ANSP); BAJA CALIFORNIA SUR: Isla Partida (AMNH, USNM); La Paz (ANSP, DMNH, USNM); Bahía Pinchilingue (USNM); Isla San Francisco (USNM); Isla San José; Punta Aqua Verde (both USNM); Isla Danzante; Isla Carmen; Isla Coronados; Bahía de San Carlos (all AMNH); SONORA: Puerto Libertad; Isla Tiburon (both USNM); Bahía Kino (MCZ). EL SALVADOR: La Libertad (ANSP, MCZ). COSTA RICA: Puerto Culebra (ANSP). PANAMA: Bay of Panama (UMMC).

Remarks: Pilsbry introduced the variety *ampullacea* for specimens possessing wider valves than those of the typical form. An examination of available material clearly shows a continuous range of variation in the width of the tegmentum in specimens from the same locality. LELOUP

Explanation of Figures 81 to 83

Figures 81–83. *Americhiton arragonites* (Carpenter, 1857), Ba-
hía Kino, Sonora, Mexico (GTW).

Figure 81. Intermediate valve VII (2.4 mm width).

Figure 82. Posterior valve (1.8 mm width).

Figure 83. Posterior valve profile.

(1941) illustrated some interesting examples of malformed
specimens.

There is an absence of specimens from Sonora to El
Salvador in the collections that I have examined. This
striking species is more common than is generally thought
and the discontinuity cannot be readily ascribed to a lack
of collecting. I cannot detect any difference between the
northern and southern specimens and the apparent hiatus
cannot be explained at this time.

This is one of the most distinctive species of this family
and cannot easily be confused with any other acanthochi-
ton. The nearest relatives of *Acanthochitona exquisita* are
A. rhodea, A. hemphilli, and *A. ferreirai;* all three species
are also large chitons with girdles encroaching on the teg-
mentum. The brick-red tegmentum and minutely spiculose
girdle both serve to separate these species from *A. exquisita.*
Large specimens of *A. hirudiniformis hirudiniformis* occa-
sionally may approximate this species in the development
of the sutural tufts and overall coloration, but *A. exquisita*
differs in its greatly reduced tegmentum.

This species is apparently locally common. MCLEAN
(1961:453) reported 30 individuals on the underside of a
single rock.

As with *Acanthochitona rhodeus* and *A. hemphilli, A. ex-
quisita* was described in the July number of *The Nautilus,*
not the *Manual of Conchology* as is generally believed. The
variety *ampullaceus* does originate from the *Manual,* how-
ever.

Americhiton Watters, gen. nov.

Type species: *Acanthochites arragonites* Carpenter, 1857,
by original designation herein.

Diagnosis: Small chitons, vermiform, tegmentum of in-
termediate valves pentagonal, each about as wide as long.
Tegmentum sculptured with convex, D-shaped pustules,
each bearing 1 or 2 macresthetes with micresthetes con-
fined to prepustular slope. Esthete innervations sand-
wiched between tegmentum and articulamentum, no myo-
stracum palleale apparent. Apophyses moderately extensive.
Slit formula 5-1-2+. Dorsal girdle elements mono- or
bimorphic; sutural tufts large but composed of relatively
few spicules; ventral spicules monomorphic, flattened in
cross-section, smooth.

Remarks: This genus superficially resembles some species
of *Craspedochiton s.l.,* but the absence of interpustular es-
thetes, which have been found in all species of *Craspe-
dochiton* that I have examined, suggests a closer relation-
ship to *Acanthochitona.* The genus *Americhiton* contains
A. arragonites from the eastern Pacific and the following
western Atlantic species: *A. andersoni* (Watters, 1981), *A.
balesae* (Abbott, 1954), and *A. zebra* (Lyons, 1988).

This genus differs from *Acanthochitona* in the form of
the pustules and the esthete distributional pattern. It has
D-shaped convex pustules rather than oval or teardrop-
shaped concave pustules, and micresthetes generally lim-
ited to the prepustular slope rather than distributed across
the pustule. The four described species are all small, ver-
miform, and limited to the New World. They form a
cohesive group of chitons quite different from other New
World species and constitute a separate genus. Vermiform
Old World species appear to belong to *Acanthochitona, e.g.,*
A. penetrans (Winckworth, 1933) and *A. shirleyi* (Ashby,
1922). FERREIRA (1985) synonymized species of this genus
with *Choneplax lata,* a cryptoplacine; this confusion ap-

Figure 84

Distribution of *Americhiton* arragonites (Carpenter, 1857).

Explanation of Figures 85 to 93

Figures 85–93. Representative denticle caps from the radulae of New World Cryptoplacidae (median to the right; measurements are for widths).

Figure 85. *Americhiton* balesae (Abbott, 1954), Galeta Point, Canal Zone (east) (RCB). 100 μm.

Figure 86. Paratype of *Americhiton* andersoni (Watters, 1981), Picquet Rocks, Bimini, Bahamas (DMNH). 100 μm.

Figure 87. *Acanthochitona angelica* (Dall, 1919), María Magdelina Id., Tres Marias Ids., Mexico (AMNH). 200 μm.

Figure 88. *Acanthochitona avicula* (Carpenter, 1864), Agua de Chale, Baja California, Mexico (AMNH). 200 μm.

Figure 89. *Acanthochitona imperatrix* Watters, 1981, La Paz, Baja California Sur, Mexico (USNM). 100 μm.

Figure 90. *Americhiton* arragonites (Carpenter, 1857), Bahía Kino, Sonora, Mexico (GTW). 100 μm.

Figure 91. *Choneplax lata* (Guilding, 1829), Galeta Point, Canal Zone (east) (RCB). 150 μm.

Figure 92. *Acanthochitona hirudiniformis hirudiniformis* (Sowerby I, 1832), Isla Pinzón (Duncan Id.), Galápagos Ids., Ecuador (GTW). 300 μm.

Figure 93. *Acanthochitona exquisita* (Pilsbry, 1893), Puertocitos, Baja California, Mexico (GTW). 300 μm.

parently arose from his misidentification of small adult chitons as juvenile specimens of larger species.

Etymology: A combination of "America" and the standard "-*chiton*" ending; the known species are confined to the Americas.

Americhiton arragonites (Carpenter, 1857)

(Figures 77–84, 90)

Acanthochites arragonites CARPENTER, 1857:190; CARPENTER, 1864:650; CARPENTER, 1872:136; PILSBRY, 1893b:25, 26; NIERSTRASZ, 1905:60; BRANN, 1966:46; pl. 12, fig. 258; KEEN, 1968:433; pl. 59, fig. 82.

Acanthochites arragonitei [sic] Carpenter: CARPENTER, 1866: 211.

Acanthochites arragonite [sic] Carpenter: CARPENTER, 1866: 211.

Acanthochitona aragonites [sic] (Carpenter): DALL, 1919:515.
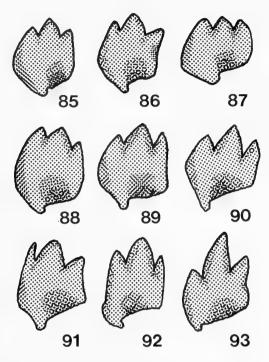
Acanthochiton arragonites (Carpenter): LELOUP, 1941:3, 9; FISCHER, 1978:37.

Acanthochitona arragonites (Carpenter): STEINBECK & RICKETTS, 1941:551; CHACE, 1958:331; KEEN, 1958:519; KEEN, 1968:433; pl. 59, fig. 92; THORPE, 1971:866; fig. 10; ABBOTT, 1974:407; SMITH & FERREIRA, 1977:94; KAAS & VAN BELLE, 1980:10; WATTERS, 1981b:175, 176; pl. 2h–j; pl. 4k; LYONS, 1988a:112; SKOGLUND, 1989:87.

"*Acanthochitona* cf. *A. arragonites* (Carpenter)": DUSHANE & SPHON, 1968:244.

Type material: Lectotype, by designation of KEEN (1968: 414), BMNH 1857.6.4.907, a loose, partially disarticulated specimen; paralectotype, four valves of another glued onto a glass strip.

Type locality: "Mazatlan," (Sinaloa, Mexico).

Description: Largest specimen, 12 mm in length. Tegmentum of intermediate valves longer than wide, pentagonal in outline. Jugum smooth, very wide. Jugal macresthetes arranged in longitudinal rows, each accompanied by 1–7 micresthetes. Latero-pleural coarsely granulose, the

pustules D-shaped. Each pustule bearing one macresthete located acentrically towards beak, with 2–4 micresthetes predominantly confined to premacresthete area. Mucro posteriorly acentric, very prominent, postmucronal slope steep and concave. Tegmentum uniformly china white, green, brown, or variegated with these colors; jugum may differ in color from latero-pleural areas.

Apophyses not extensive. Slit formula 5-1-2. Articulamentum white or green, tinged with rose towards beak.

Dorsum of girdle velvety, covered with minute, finely ribbed, bent monomorphic elements. Dorsum white, mottled with green and brown. Sutural tufts and marginal fringe well-developed, colored translucent white or green. Marginal fringe bimorphic; larger elements finely ribbed; both bent.

Distribution: Intertidally to 20 m from Sonora, Mexico to Salinas, Ecuador.

Material examined: MEXICO: BAJA CALIFORNIA SUR: Cabo San Lucas (USNM); SONORA: Guaymas, N of Bahía San Carlos, Ensenada Lalo (DMNH); Bahía Kino (GTW). ECUADOR: Salinas (GTW).

Remarks: Specimens of this species are rare in collections and are usually misidentified as small examples of *Acanthochitona avicula*. PILSBRY (1893b:26) remarked "it would be difficult to find a shell of such surpassing beauty"; nevertheless he did not illustrate it, and the species remained unfigured until BRANN (1966), 73 years later.

This species is most closely related to *Americhiton andersoni* and *A. zebra*, all of which have the pustules of the intermediate valves in a radiating pattern from the jugum; in *A. balesae*, the pustules parallel the jugum.

ACKNOWLEDGMENTS

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New Species of Late Cretaceous Cypraeacea (Mollusca: Gastropoda) from California and Mississippi, and a Review of Cretaceous Cypraeaceans of North America

by

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Abstract. Cypraeacean mollusks are rare in Cretaceous deposits of North America. Only 15 species are recognized, of which four are new and are described herein. Six species of *Palaeocypraea s.s.* have been previously described, and *Palaeocypraea (P.) fontana* (Anderson, 1958) from the Lower Cretaceous (uppermost Lower Albian), Budden Canyon Formation, Shasta County, California, is the earliest known cypraeacean from the Western Hemisphere. *Bernaya s.s.* is represented by two species and *Bernaya (Protocypraea)* comprises five species. *Eocypraea s.s.* is represented by two species.

New species described herein are as follows: *Bernaya (B.) crawfordcatei* from the Upper Cretaceous (Campanian/Maastrichtian), Point Loma Formation, San Diego County, California; *Bernaya (Protocypraea) mississippiensis* from the Upper Cretaceous (Campanian), Coffee Formation, Lee County, Mississippi; *B. (P.) rineyi* from the Upper Cretaceous (Campanian/Maastrichtian), Point Loma Formation, San Diego County, California; and *Eocypraea (E.) louellae* from the Upper Cretaceous (Turonian), Yolo Formation, Yolo County, California. *Eocypraea (E.) louellae* is the earliest known ovulid from the Western Hemisphere.

INTRODUCTION

Four new species of cypraeacean gastropods, rare in Cretaceous deposits of North America, are described from localities in San Diego and Yolo counties, California, and Lee County, Mississippi (Figure 1). Two of the new species are from the Upper Cretaceous (Campanian/Maastrichtian), Point Loma Formation (Rosario Group), near Carlsbad, northern San Diego County, southern California; the third is from the Upper Cretaceous (Turonian), Yolo Formation of the Great Valley Series, Yolo County, northern California. A fourth new species is from the Upper Cretaceous (Campanian), Coffee Formation (Selma Group), Lee County, northeastern Mississippi. This paper describes and illustrates these new species as well as illustrating and providing a brief synopsis of the previously described North American cypraeacean species.

Historical Review

The first cypraeacean species described from the Cretaceous of North America was *Cypraea mortoni* Gabb, 1860. *Cypraea squyeri* Campbell, 1893, from Montana and a similar species, *Cypraea suciensis* Whiteaves, 1895, from Sucia Island, Washington, were subsequently described. SCHILDER (1932) separated species from Alabama and New Jersey, both previously considered to be *Cypraea mortoni,* and proposed *Palaeocypraea burlingtonensis* for the New Jersey species. In a survey of the Navarro Group of Texas, STEPHENSON (1941) described two new species: *Cypraea nuciformis* and *Cypraea gracilis* (*Cypraea gracilis* Stephenson, preoccupied, was subsequently renamed *Cypraea corsicanana* Stephenson, 1948). INGRAM (1942, 1947a, b) included Cretaceous species in his reviews of North American fossil and living cypraeaceans. ANDERSON (1958)

Figure 1

Index maps showing locations of type localities of new species of Cretaceous cypraeids described herein. Localities listed are described in the Appendix—Localities Cited.

described *Cypraea gualalaensis, Cypraea berryessae,* and *Cypraea fontana* from northern California. Anderson also introduced the name *Cypraea argonautica* for a specimen from Oregon he had previously identified as *Erato veraghoorensis* Stoliczka, 1867. Most recently, *Cypraea grooti* Richards & Shapiro, 1963, was described from northern Delaware.

Cypraeacean Biogeography

Recent cypraeaceans have their greatest diversity and abundance in warm tropical oceans; warm temperate seas seldom support more than a single species. Cretaceous species ranged as far north as San Juan County, Washington (49°45′N) in North America and Valkenburg, The Netherlands (50°52′N) in Europe. The Cretaceous distribution of cypraeaceans supports the concept of both broad tropical and subtropical to warm-temperate climatic belts (SOHL, 1971).

Mesozoic Cypraeacean Paleontology

The earliest known cypraeaceans, *Palaeocypraea (P.) tithonica* (Stefano, 1882) and *Bernaya (B.) gemmellaroi* (Stefano, 1882), are from Upper Jurassic (Tithonian) strata near Termini Imerese, Sicily, Italy. Cretaceous cypraeaceans have been found in Europe, India, South Africa, Iran, North America, and Brazil (SCHILDER & SCHILDER, 1971). SCHILDER & SCHILDER (1971) recognize 69 species of Cretaceous cypraeaceans, 43 of which are from uppermost Cretaceous (Campanian through Maastrichtian)

strata, the cypraeacean Mesozoic peak in terms of both numbers of species and geographic distribution.

Genera and subgenera found in North America are *Palaeocypraea s.s., Bernaya s.s., Bernaya (Protocypraea),* and *Eocypraea s.s.* (Figure 2). *Palaeocypraea* is known from Upper Jurassic (Tithonian) through Upper Paleocene (Thanetian) strata in Europe, South Africa, North America, and Brazil (SCHILDER & SCHILDER, 1971). In the North American Cretaceous it is represented by six species. *Bernaya s.s.* is known from Upper Jurassic (Tithonian) through Lower Oligocene (Lattorfian) strata in Europe, India, Iran, North America, and Brazil (SCHILDER & SCHILDER, 1971). Two species, one of them new, are found in the North American Cretaceous. *Bernaya (Protocypraea)* is known from Lower Cretaceous (Barremian) to Recent and is found in Europe, India, Iran, and western North America. *Protocypraea* is represented by a single living species, *Bernaya (Protocypraea) teulerei* Cazenavette, 1846 (=*Cypraea leucostoma* Gaskoin, 1843, *non* Gmelin, 1791; =*B. (P.) hidalgoi* (Shaw, 1909)) from the Gulf of Oman. *Bernaya (P.)* is represented by five species in the Cretaceous of North America, two of which are new. *Eocypraea s.s.* is known from Upper Cretaceous (Cenomanian) through Lower Oligocene (Lattorfian) strata in Europe, India, Iran, New Zealand, South Africa, Indonesia, North America, and South America (SCHILDER & SCHILDER, 1971). Two species of *Eocypraea s.s.,* one of them new, are from the Cretaceous of North America.

Abbreviations used for institutional catalogue and lo-

PERIOD	EPOCH	AGE	PICKS (Ma)	PACIFIC COAST	WESTERN INTERIOR AND GULF COAST	ATLANTIC COAST
			— 66.4			
CRETACEOUS	LATE	MAASTRICHTIAN		B. (B.) crawfordcatei / B. (P.) gualalaensis / B. (P.) rineyi	E. mortoni / P. corsicanana / P. nuciformis / P. squyeri	P. grooti
			— 74.5			
		CAMPANIAN		P. suciensis	B. (P.) mississippiensis	B. (B.) burlingtonensis
			— 84.0			
		SANTONIAN	— 87.5			
		CONIACIAN	— 88.5			
		TURONIAN		E. louellae / B. (P.) argonautica / B. (P.) berryessae		
			— 91.0			
		CENOMANIAN	— 97.5			
	EARLY	ALBIAN		P. fontana		
		APTIAN	— 113.0			
			— 119.0			
		NEOCOMIAN	— 144.0			

Figure 2

Relative chronologic and geographic distribution of North American Cretaceous cypraeids. Picks (Ma) = Radiometric dates (not to scale) from Geological Society of America, Decade of North American Geology [DNAG] time scale.

cality numbers are as follows: ANSP, Academy of Natural Sciences of Philadelphia; CAS, California Academy of Sciences, San Francisco; CIT, California Institute of Technology (collection now at LACMIP); GSC, Geological Survey of Canada, Ottawa; LACMIP, Los Angeles County Museum of Natural History; MGS, Mississippi Geological Survey, Jackson; SDSNH, San Diego Society of Natural History; USGS, United States Geological Survey, Washington; and USNM, National Museum of Natural History, Smithsonian Institution, Washington.

Measurement parameters are defined as follows: length = greatest distance between anterior and posterior ends; width = greatest distance between lateral margins; and height = greatest distance between base and dorsum.

STRATIGRAPHY

Point Loma Formation

The type section for the Point Loma Formation (KENNEDY & MOORE, 1971:711–713) is at Point Loma, San Diego County, California. Its stratigraphic position is near the Campanian/Maastrichtian boundary based upon benthic foraminifera (SLITER, 1968) and mollusks (BANNON et al., 1989). A magnetic reversal in the Point Loma Formation at La Jolla, California, suggests that the formation is mainly early Maastrichtian in age (BANNON et al., 1989). Strata at Carlsbad, California, have been correlated with the Point Loma and La Jolla sections (SLITER, 1968). The mollusks at Carlsbad suggest a more near-shore environment for the Carlsbad strata than for much of the Point Loma and La Jolla strata. Diagnostic molluscan species common to all three areas—e.g., *Baculites lomaensis* Anderson, 1958, *Pachydiscus (Neodesmoceras) catarinae* (Anderson & Hanna, 1935), and *Perissitys colocara* Popenoe & Saul, 1987—suggest that these sections are of equivalent age. Calcareous nannofossils, benthic foraminifera, and palynomorphs from Carlsbad also sug-

gest a Campanian to Maastrichtian age (M. V. FILEWICZ et al., 1989, personal communication). A 17-m thick section of the Point Loma Formation near Carlsbad consists of shale and interbedded sandstones that contain a diverse and locally rich molluscan fauna (LOCH, 1989). Fossils in the deposit represent a distinct inner shelf assemblage in water less than 140 m deep (SLITER, 1968).

Yolo Formation

The Upper Cretaceous (Turonian), Yolo Formation of KIRBY (1943:285–287) was named for extensive exposures along the west side of the Sacramento Valley in Yolo County, northern California. Petrologic evidence suggests that the randomly interbedded mudstones, shales, and sandstones of the Yolo Formation were deposited as basin-plain turbidite deposits within the Great Valley forearc basin sequence (INGERSOL et al., 1977).

Coffee Formation

The Coffee Formation of the Selma Group was named by SAFFORD (1864:361–363) for exposures at Coffee Landing, Hardin County, Tennessee. Sandstone units in the Tupelo Tongue of the Coffee Formation demonstrate a cyclical sedimentation pattern related to four periods of delta progadation and abandonment (DOCKERY & JENNINGS, 1988). Excavations within the last 15 yr in northeastern Lee County, Mississippi, have exposed very fossiliferous sections of the Upper Cretaceous (Campanian), Coffee Formation (DOCKERY, 1988).

MATERIALS AND METHODS

Thirty-one cypraeacean specimens from the San Diego Society of Natural History, Invertebrate Paleontology collection were borrowed for this project. Two undescribed and one previously described species were determined. A subsequent search of the Los Angeles County Museum of

Natural History, Invertebrate Paleontology collection yielded an additional undescribed species, two specimens of *Bernaya (Protocypraea) argonautica,* and two cypraeacean fragments of undetermined generic affinity. A fourth undescribed species was borrowed from the Mississippi Geologic Survey. Undescribed specimens were compared to the holotypes of all previously described North American species, which are figured herein for comparison. Comparisons were also made with published illustrations of species from regions other than North America. Matrix from the apertures of several specimens was carefully removed with permission of the lending institutions.

SYSTEMATICS

The classification herein follows that of SCHILDER & SCHILDER (1971) with the exception of the Recent southwestern Australian species *Bernaya catei* Schilder, 1963. BURGESS (1970, 1985) and WALLS (1979) correctly placed *B. catei* in synonymy with *Zoila (Zoila) venusta* (Sowerby, 1846) based upon similar anatomical and radular characteristics. The genus *Zoila* of JOUSSEAUME (1884), which ranges from the Lower Miocene to the Recent of Australia, India, Indonesia, and Tasmania, may be a descendant of *Bernaya* (WENZ, 1941).

SYSTEMATIC PALEONTOLOGY

Superfamily CYPRAEACEA Rafinesque, 1815

Family CYPRAEIDAE Rafinesque, 1815

Subfamily BERNAYINAE Schilder, 1927

Genus *Palaeocypraea* Schilder, 1928

Type species: *Cypraeacites spiratus* Schlotheim, 1820, by original designation. Lower Paleocene (Danian), Faxe, Denmark.

Diagnosis: Shell small to medium in size, elongated, spire broad and partially covered, aperture wide with deep terminal canals and fine dentition, fossula broad, concave, and smooth.

Subgenus *Palaeocypraea s.s.*

Palaeocypraea (Palaeocypraea) corsicanana
(Stephenson, 1948)

Figures 3, 4)

Cypraea gracilis STEPHENSON, 1941:314–315, pl. 59, figs. 12–13. Not *Cypraea gracilis* Gaskoin, 1848.
Cypraea corsicanana STEPHENSON, 1948:642 [new name for *Cypraea gracilis* Stephenson, 1941].
Palaeocypraea (Palaeocypraea) squyeri corsicanana (Stephenson, 1948: SCHILDER & SCHILDER, 1971:25, 107.

Type material: Holotype, USNM 20894. The holotype measures 14.2 mm in length, 10 mm in width, and 7.8 mm in height.

Type locality: USGS loc. 518, near Postoak Creek, north edge of Corsicana, Navarro County, Texas. Upper Cretaceous (Maastrichtian), Nacatoch Sand, Navarro Group.

Remarks: *Palaeocypraea squyeri* (Campbell, 1893) has deeper terminal canals and is more elongate than *Palaeocypraea corsicanana,* and should be considered a separate species.

Palaeocypraea (Palaeocypraea) fontana
(Anderson, 1958)

(Figures 5, 6)

Cypraea fontana ANDERSON, 1958:177, pl. 21, figs. 15, 16.
Palaeocypraea (Palaeocypraea) korycanensis fontana (Anderson, 1958): SCHILDER & SCHILDER, 1971:25, 116.

Type material: Holotype, CAS 1345.04. The holotype measures 27.8 mm in length, 16.8 mm in width, and 11.1 mm in height.

Type locality: CAS loc. 1345, Texas Springs, 3.2 km east of Horsetown, on road leading to Centerville, Shasta County, California. Lower Cretaceous (uppermost lower Albian) (L. R. Saul, 1989, personal communication), Budden Canyon Formation.

Remarks: *Palaeocypraea korycanensis* (Weinzettl, 1910) from Korycany, Czechoslovakia, is more elongate and less globose than *Palaeocypraea fontana* (Anderson, 1958) and is considered a separate species. *Palaeocypraea fontana* is the earliest cypraeacean found in the Western Hemisphere.

Palaeocypraea (Palaeocypraea) grooti
(Richards & Shapiro, 1963)
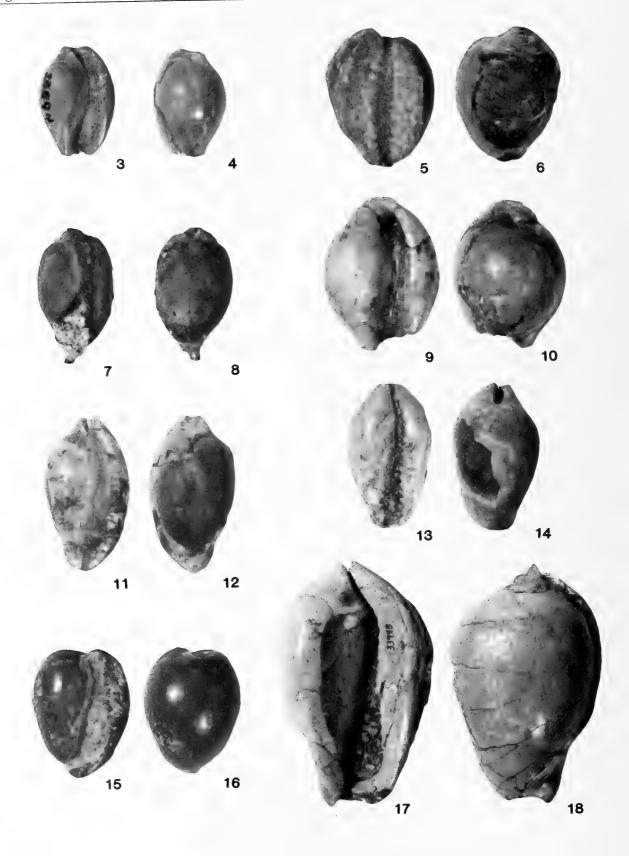
(Figures 7, 8)

Cypraea grooti RICHARDS & SHAPIRO, 1963:12, pl. 4, fig. 3a–c; RICHARDS, 1968:140; OWENS *et al.*, 1970:45.
Palaeocypraea (Palaeocypraea) squyeri grooti (Richards & Shapiro, 1963): SCHILDER & SCHILDER, 1971:25, 120.

Type material: Holotype, ANSP 30838. The holotype measures 17.5 mm in length, 10.1 mm in width, and 7.9 mm in height.

Type locality: Station 6 of GROOT *et al.* (1954), Biggs Farm, south bank Chesapeake and Delaware Canal, 2.41 km east of crossing of U.S. Highway 13 and the canal at St. Georges, New Castle County, Delaware. Upper Cretaceous (lower Maastrichtian), Mt. Laurel-Navesink Formation.

Remarks: Represented by a single poorly preserved internal mold that does not resemble *Palaeocypraea squyeri* (Campbell, 1893). *Palaeocypraea grooti* is more globose and less elongate than *P. squyeri* and, although treated as a subspecies of the latter by SCHILDER & SCHILDER (1971: 25), they are considered separate species.

Palaeocypraea (*Palaeocypraea*) *nuciformis*
(Stephenson, 1941)

(Figures 9, 10)

Cypraea nuciformis STEPHENSON, 1941:314, pl. 59, figs. 8
(holotype), 10–11 (paratypes).
Palaeocypraea (*Palaeocypraea*) *suecica nuciformis* (Stephenson,
1941): SCHILDER & SCHILDER, 1971:25, 138.

Type material: Holotype, USNM 76988, and two paratypes, USNM 21007. The holotype measures 24 mm in length, 18.1 mm in width, and 14.7 mm in height.

Type locality: USGS loc. 761, in the vicinity of Kaufman, Kaufman County, Texas. Upper Cretaceous (Maastrichtian), Nacatoch Sand, Navarro Group.

Remarks: The holotype and two paratypes are from the same locality. *Palaeocypraea nuciformis* has a wider aperture and is more globose than *P. suecica* Schilder, 1928, from Denmark and they are considered separate species.

Palaeocypraea (*Palaeocypraea*) *squyeri*
(Campbell, 1893)

(Figures 11, 12)

Cypraea squyerii CAMPBELL, 1892:50–51, *nomen nudum*.
Cypraea squyeri CAMPBELL, 1893:52, pl. 2, figs. 1, 2; INGRAM,
1942:16, pl. 3, figs. 3, 4; INGRAM 1947a:59–60, pl. 2,
figs. 11, 12; INGRAM, 1947b:13; RICHARDS, 1968:190.
Palaeocypraea squyeri (Campbell, 1893): SCHILDER, 1932:
110.
Palaeocypraea (*Palaeocypraea*) *squyeri* (Campbell, 1893):
SCHILDER & SCHILDER, 1971:25, 157.

Type material: Holotype, ANSP 13536. The holotype measures 20.1 mm in length, 11 mm in width, and 8.9 mm in height.

Type locality: Near Mingusville (now Wibaux), Dawson County (now in Wibaux County), Montana. Upper Cretaceous (Maastrichtian), Fox Hills Formation.

Remarks: This species is represented only by the well preserved holotype. *Palaeocypraea squyeri* is similar to *P. suciensis* (Whiteaves, 1895), but is more elongate and has a shallower posterior terminal canal than the latter, and should be considered a separate species.

Palaeocypraea (*Palaeocypraea*) *suciensis*
(Whiteaves, 1895)

(Figures 13, 14)

Cypraea suciensis WHITEAVES, 1895:127–128, pl. 3, fig. 5;
WHITEAVES, 1903:357; WHITNEY, 1928:154; INGRAM,
1942:16; INGRAM, 1947a:60–61; INGRAM, 1947b:13;
BOLTEN, 1965:15.
Palaeocypraea suciensis (Whiteaves, 1895): SCHILDER, 1932:
110.
Palaeocypraea (*Palaeocypraea*) *squyeri suciensis* (Whiteaves,
1895): SCHILDER & SCHILDER, 1971:25, 160.

Type material: Holotype, GSC 5937. The holotype measures 19.5 mm in length, 11.9 mm in width, and 9.5 mm in height.

Type locality: Sucia Island, San Juan County, Washington. Upper Cretaceous (lower late Campanian), Cedar District Formation, Nanaimo Group.

Remarks: This species is based only on the well preserved holotype. *Palaeocypraea suciensis* differs from *P. squyeri* (Campbell, 1893) by its less elongate shell and deeper posterior terminal canal, and should be considered a separate species.

Genus *Bernaya* Jousseaume, 1884

Type species: *Cypraea media* Deshayes, 1835, by original designation. Upper Middle Eocene (Bartonian Stage), Auvers-sur-Oise, Val-d'Oise (northwest of Paris).

Diagnosis: Shell medium to large size, anterior end somewhat carinate, dorsum smooth, spire of medium height and partially covered, aperture wide, sides rounded, anterior and posterior canals deep, fossula smooth, concave, wide.

Subgenus *Bernaya s.s.*

Diagnosis: Shell more elongate and aperture less sinuous than in *Bernaya* (*Protocypraea*).

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Explanation of Figures 3 to 18

Figures 3, 4. *Palaeocypraea* (*Palaeocypraea*) *corsicanana* (Stephenson, 1948), holotype, USNM 20894, from USGS loc. 518, ×2.0. Figures 5, 6. *Palaeocypraea* (*Palaeocypraea*) *fontana* (Anderson, 1958), holotype, CAS 1345.04, from CAS loc. 1345, ×1.3. Figures 7, 8. *Palaeocypraea* (*Palaeocypraea*) *grooti* (Richards & Shapiro, 1963), holotype, ANSP 30838, from station 6 of GROOT *et al.* (1954), ×2.0. Figures 9, 10. *Palaeocypraea* (*Palaeocypraea*) *nuciformis* (Stephenson, 1941), holotype, USNM 76988, from USGS loc. 761, ×1.7. Figures 11, 12. *Palaeocypraea* (*Palaeocypraea*) *squyeri* (Campbell, 1893), holotype, ANSP 13536, from Mingusville (now Wibaux), Montana, ×2.0. Figures 13, 14. *Palaeocypraea* (*Palaeocypraea*) *suciensis* (Whiteaves, 1895), holotype, GSC 5937, from Sucia Island, Washington, ×2.0. Figures 15, 16. *Bernaya* (*Bernaya*) *burlingtonensis* (Schilder, 1932), holotype, ANSP 13537, from Burlington County, New Jersey, ×2.0. Figures 17, 18. *Bernaya* (*Bernaya*) **crawfordcatei** sp. nov., holotype, SDSNH 33998, from SDSNH loc. 3392, ×0.9.

Bernaya (Bernaya) burlingtonensis
(Schilder, 1932)

Figures (15, 16)

Cypraea (Aricia) mortoni Gabb, 1860: GABB, 1861:104 [in part]; WHITFIELD, 1892a:120, 291, pl. 15, figs. 1–3; WHITFIELD, 1892b:120, 291, pl. 15, figs. 1–3; WHITNEY, 1928:154. Not *Cypraea mortoni* Gabb, 1860 [=*Eocypraea (E.) mortoni* (Gabb), *q.v.*].

Cypraea mortoni Gabb, 1860: MEEK, 1864:19 [in part]; COOK, 1868:729; JOHNSON, 1905:23; WELLER, 1907:722–723 [in part], pl. 84, figs. 1–2; WHITNEY, 1928:154 [in part]; RICHARDS & RAMSDELL, 1962:47, pl. 53, fig. 9, pl. 64, fig. 6. Not *Cypraea mortoni* Gabb, 1860.

Palaeocypraea burlingtonensis SCHILDER, 1932:111 [new name for *Cypraea "mortoni"* of Gabb, 1861]: SCHILDER, 1958: 162.

Cypraea cf. *C. mortoni* Gabb, 1860: Owens *et al.,* 1970:42. Not *Cypraea mortoni* Gabb, 1860.

Bernaya (Bernaya) burlingtonensis (Schilder, 1932): SCHILDER & SCHILDER, 1971:26, 101.

Type material: Holotype, ANSP 13537. The holotype measures 16.5 mm in length, 12.9 mm in width, and 9.6 mm in height.

Type locality: Burlington County, New Jersey. Upper Cretaceous (upper Campanian), Mt. Laurel-Navesink Formation.

Remarks: *Bernaya (B.) burlingtonensis* is represented by at least three specimens. An internal mold was figured by WHITFIELD (1892a, b) as *Cypraea (Aricia) mortoni* Gabb, 1860. Based upon a comparison to the ANSP specimen, this is the holotype. A second specimen was illustrated by WELLER (1907) as *Cypraea mortoni* Gabb from Atlantic Highlands, Monmouth County, New Jersey. A third specimen was collected from the Upper Cretaceous (Campanian) Marshalltown Formation (USGS loc. 17702) by C. W. Carter (OWENS *et al.,* 1970) near the Chesapeake and Delaware Canal, New Castle County, Delaware. SCHILDER (1932) separated these Campanian specimens—previously identified with *Cypraea mortoni,* the Maastrichtian species—based on a similar, but less globose, internal mold from Prairie Bluff, Alabama.

*Bernaya (Bernaya) **crawfordcatei*** Groves, sp. nov.

(Figures 17, 18)

Diagnosis: A *Bernaya* of large size, anterior and posterior canals deep, spire of medium height, fossula smooth concave, anterior and posterior terminal ridges prominent extending to margins.

Description: Shell large, somewhat constricted anteriorly; maximum height and width posterior to center; spire of medium height, partially covered; dorsum somewhat flattened; aperture wide, slightly S-shaped; denticulation coarse, with smooth interstices, outer lip with 16 teeth that become stronger posteriorly; outer lip with prominent anterior and posterior terminal ridges extending to anterior and posterior margins; posterior terminal ridge extending

to base of spire; anterior terminal ridge forming slight marginal callus.

Comparison: The new species most similar to *Bernaya (Protocypraea) gualalaensis* (ANDERSON, 1958:176, pl. 63, fig. 2–2b) from the Upper Cretaceous (lower Maastrichtian), Gualala Group, Mendocino County, California. *Bernaya (B.) **crawfordcatei*** differs from *B. (P.) gualalaensis* by its larger size, coarser denticulation, wider base, terminal ridges that do not extend onto the spire, slight anterior marginal callus, deeper anterior and posterior canals, and a gently sloping anterior profile.

Discussion: Post-depositional crushing has damaged the fossula and inner lip dentition. Generic and subgeneric assignment are based on its large size, wide aperture, deep anterior and posterior terminal canals, and spire of medium height. *Bernaya (B.) **crawfordcatei*** is much larger than other North American Cretaceous cypraeaceans and exceeds the next largest species, *B. (Protocypraea) gualalaensis* (Anderson, 1958), by 22 mm in length.

Material: The new species is represented by two specimens. The holotype is slightly crushed, but otherwise well preserved. A second specimen is a poorly preserved internal mold with minor amounts of original shell material.

Type material: Holotype, SDSNH 33998. The holotype measures 72.9 mm in length, 45.8 mm in width, and 30.2 mm in height.

Type locality: SDSNH loc. 3392, near Carlsbad, northern San Diego County, southern California. Upper Cretaceous (Campanian/Maastrichtian), Point Loma Formation.

Etymology: The species is named in honor of the late Crawford N. Cate, in recognition of his valuable contributions to cypraeacean studies.

Subgenus *Protocypraea* Schilder, 1927

Type species: *Eocypraea orbignyana* Vredenburg, 1920, by original designation. Upper Cretaceous (Turonian through Santonian), Trichinopoly Group, Kullygoody, southern India.

Diagnosis: Shell small to medium in size, shape moderately pyriform, somewhat constricted anteriorly, fossula smooth, concave, wide.

Bernaya (Protocypraea) argonautica
(Anderson, 1958)

(Figures 19, 20)

Erato vergahoörensis [*sic*] (?) Stol.[iczka, 1867]: ANDERSON, 1902:75–76, pl. 9, figs. 181, 182. Not *Erato veraghoorensis* Stoliczka, 1867 [=*Bernaya (P.) veraghoorensis*].

Cypraea argonautica ANDERSON, 1958:177, pl. 21, fig. 4–4a.

Bernaya (Protocypraea) argonautica (Anderson, 1958): SCHILDER & SCHILDER, 1971:26, 96.

Type material: Holotype, CAS 61856.05 [*ex* CAS 42]. The holotype is a partially pyritized specimen that mea-

sures 21.5 mm in length, 19 mm in width, and 13.6 in height. The holotype was damaged in the 1906 San Francisco fire, but was recovered and preserved in the CAS Type Collection as CAS 42 (ANDERSON, 1958).

Type locality: CAS loc. 61856 [*ex* CAS loc. 445-A], Fitch Ranch (formerly Smith Ranch), 3.2 km west of Phoenix, Jackson County, Oregon. Upper Cretaceous (Cenomanian or lower Turonian) (L. R. Saul, 1989, personal communication), Blue Gulch Member, Hornbrook Formation.

Remarks: Two specimens of *Bernaya* (*P.*) *argonautica* from LACMIP loc. 10903 are from the Turonian, near Ashland, Jackson County, Oregon. Although similar, *B.* (*P.*) *veraghoorensis* (Stoliczka, 1867) from southern India is more elongate than *B.* (*P.*) *argonautica,* and is treated as a separate species.

Bernaya (*Protocypraea*) *berryessae*
(Anderson, 1958)

(Figures 21, 22)

Cypraea berryessae ANDERSON, 1958:176, pl. 63, fig. 2–2b.
Bernaya (*Protocypraea*) *berryessae* (Anderson, 1958): SCHILDER & SCHILDER, 1971:26, 99.

Type material: Holotype, CAS 31918.02 [*ex* CAS 10677]. The holotype measures 18 mm in length, 13.1 mm in width, and 9.8 mm in height.

Type locality: CAS loc. 31918, Thompson Canyon area, Yolo County, northern California. Upper Cretaceous (Turonian), Yolo Formation (POPENOE *et al.,* 1987).

Remarks: Two well preserved topotypes were also examined.

Bernaya (*Protocypraea*) *gualalaensis*
(Anderson, 1958)

(Figures 23–26)

Cypraea gualalaensis ANDERSON, 1958:176, pl. 62, fig. 8–8a.
Bernaya (*Protocypraea*) *kayei gualalaensis* (Anderson, 1958): SCHILDER & SCHILDER, 1971:26, 120.
Cypraea guadelensis [*sic*] Anderson, 1958: SUNDBERG & RINEY, 1984:105, fig, 3, no. 6.

Type material: Holotype, CAS 61918.01 [*ex* CAS 10679]. The holotype measures 50.2 mm in length, 32.4 mm in width, and 22.1 mm in height.

Type locality: CAS loc. 61918 [*ex* S. G. Clark loc. 251], near Gualala, Mendocino County, California. Upper Cretaceous (lower Maastrichtian), Gualala Group.

Remarks: This species is represented by a somewhat well preserved holotype and 23 specimens from the Upper Cretaceous (Campanian/Maastrichtian), Point Loma Formation, SDSNH locs. 3162, 3162-A, 3162-B, 3162-M, 3392, 3405, and 3454 near Carlsbad, San Diego County, California. The specimen figured by SUNDBERG & RINEY (1984:105, fig. 3, no. 6), SDSNH 25947, measures 36.7

mm in length, 22.3 mm in width, and 19.4 mm in height. Another specimen from Carlsbad (Figures 25, 26) measures 38.4 mm in length, 23.6 mm in width, and 19 mm in height. The Carlsbad specimens are excellently preserved and display original shell material. *Bernaya* (*Protocypraea*) *kayei* (Forbes, 1846) from southern India, is similar to *B.* (*P.*) *gualalaensis* but is more globose and less elongate, and is treated here as a separate species.

Bernaya (*Protocypraea*) *mississippiensis* Groves, sp. nov.

(Figures 27, 28)

Bernaya (*s.l.*) new species: DOCKERY, 1988:19, fig. 3.

Diagnosis: Pyriform *Protocypraea,* anterior and posterior basal terminal ridges prominent, fossula, concave, smooth.

Description: Shell moderately inflated, slightly elongate, of small size, constricted anteriorly; spire covered, dorsum moderately arched; maximum height near midpoint of shell; maximum width slightly posterior of center; aperture slightly S-shaped, denticulation fine with smooth interstices, outer lip with 20 teeth, inner lip with 17 teeth; fossula smooth and concave; all surfaces smooth and glossy; anterior and posterior basal terminal ridges prominent; anterior and posterior terminal canals deep.
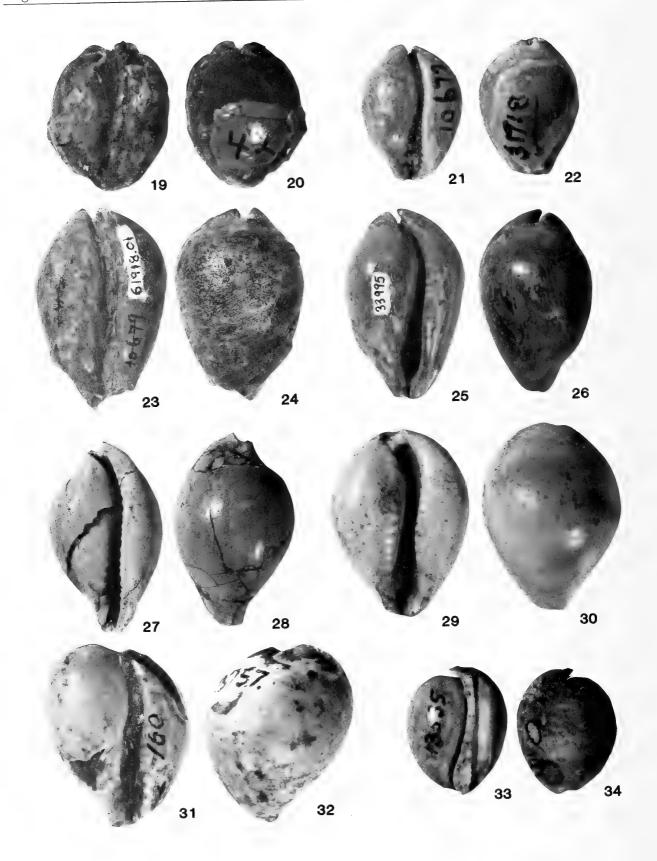
Comparison: The new species is most similar to *Bernaya* (*Protocypraea*) *rineyi* sp. nov. from the Upper Cretaceous (Campanian/Maastrichtian), Point Loma Formation, San Diego County, southern California, and to *Eocypraea newboldi* (FORBES, 1846:134, pl. 12, fig. 121) from the Upper Cretaceous (Turonian through Santonian) Trichinopoly Group of southern India. *Bernaya* (*P.*) *mississippiensis* differs from both in having more numerous apertural teeth, deeper anterior and posterior terminal canals, a less inflated dorsum, and prominent anterior and posterior basal terminal ridges.

Discussion: The excellent preservation allows for unequivocal generic and subgeneric assignment. *Bernaya* (*P.*) *mississippiensis* is quite different from other Cretaceous cypraeids from the Gulf Coast region of the United States and is the first cypraeacean species reported from the upper reaches of the Mississippi Embayment (DOCKERY, 1988).

Material: Represented by the well preserved holotype and a sub-adult paratype, both of which display original shell material.

Type material: Holotype USNM 446797, paratype USNM 446798. The holotype measures 21.5 mm in length, 13.7 mm in width, and 9.8 mm in height. The paratype measures 15.9 mm in length, 10.5 mm in width, and 8.4 mm in height.

Type locality: MGS loc. 129, northern Lee County, Mississippi. The holotype and paratype were collected from the Upper Cretaceous (Campanian), "Chapelville fossiliferous horizon" within the Tupelo Tongue sequence of the Coffee Formation near Chapelville, Mississippi.

Etymology: This species is named after the state of Mississippi.

Bernaya (Protocypraea) rineyi Groves, sp. nov.

(Figures 29, 30)

Diagnosis: Pyriform *Protocypraea*, anterior and posterior canals shallow, aperture slightly S-shaped, fossula, smooth, concave.

Description: Shell inflated-pyriform, of small size, constricted anteriorly; spire nearly covered; dorsum highly arched; maximum height near midpoint of shell; maximum width posterior of center; aperture slightly S-shaped, narrowing near midpoint and widening toward anterior end; denticulation coarse with smooth interstices, outer lip with 13 teeth that increase in strength posteriorly, inner lip with 12 teeth; fossula concave, smooth, wide; anterior and posterior terminal canals shallow; all surfaces smooth and glossy.

Comparison: The new species is most similar to *Bernaya (Protocypraea) berryessae* (ANDERSON, 1958:176, pl. 65, fig. 2–2b) from the lower Upper Cretaceous (Turonian) of Yolo County, California, but differs from the latter by its smaller size, wider, slightly S-shaped aperture, shallower anterior and posterior canals, and fewer teeth on the outer and inner lips.

Discussion: The excellent preservation displayed in the holotype allows for unequivocal generic and subgeneric assignments. Not only is *Bernaya (Protocypraea) rineyi* different from all other Cretaceous cypraeaceans from North America, but it is much younger than any similar species.

Material: Six specimens include the excellently preserved complete holotype, four poorly preserved crushed, incomplete specimens, and a single posterior fragment. All specimens appear to display original shell material.

Type material: Holotype, SDSNH 34008. The holotype measures 12.3 mm in length, 9.1 mm in width, and 7.1 mm in height.

Type locality: The holotype is from SDSNH loc. 3392 and the other specimens are from SDSNH locs. 3162-B and 3392. All of the specimens were collected from the Upper Cretaceous (Campanian/Maastrichtian), Point Loma Formation, near Carlsbad, northern San Diego County, California.

Etymology: This species is named after Bradford O. Riney (SDSNH) who collected not only the holotype, but numerous important fossils from southern California and northern Baja California, Mexico.

Family OVULIDAE Fleming, 1828

Subfamily EOCYPRAEINAE Schilder, 1924

Genus Eocypraea Cossmann, 1903

Type species: *Cypraea inflata* Lamarck, 1802, by original designation. Middle Eocene (Lutetian–Bartonian Stages), Paris Basin, France.

Diagnosis: Inflated-pyriform shell of small to medium size; spire involute; narrow elongate aperture; fossula broad, smooth, concave.

Subgenus Eocypraea s.s.

Eocypraea (Eocypraea) louellae Groves, sp. nov.

(Figures 31, 32)

Diagnosis: An *Eocypraea* with highly inflated shell, coarse denticulation, and slightly S-shaped aperture.

Description: Shell highly inflated, of small size, constricted anteriorly; spire partially covered; dorsum highly arched; maximum height slightly posterior of center; maximum width posterior of center; aperture slightly S-shaped; denticulation coarse with smooth interstices; outer lip with two teeth; fossula smooth, concave; all surfaces smooth, glossy; posterior columella highly inflated; anterior and posterior terminal canals shallow.

Comparison: The new species is most similar to *Eocypraea newboldi* (FORBES, 1846:134, pl. 12, fig. 21) from Upper Cretaceous (Turonian through Santonian), Trichinopoly

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Explanation of Figures 19 to 34

Figures 19, 20. *Bernaya (Protocypraea) argonautica* (Anderson, 1958), holotype, CAS 61856.05, from CAS loc. 61856, ×2.0. Figures 21, 22. *Bernaya (Protocypraea) berryessae* (Anderson, 1958), holotype, CAS 31918.02, from CAS loc. 31918, ×2.0. Figures 23, 24. *Bernaya (Protocypraea) gualalaensis* (Anderson, 1958), holotype, CAS 61918.01, from CAS loc. 61918, ×1.0. Figures 25, 26. *Bernaya (Protocypraea) gualalaensis* (Anderson, 1958), hypotype, SDSNH 33995, from SDSNH loc. 3405, ×1.3. Figures 27, 28. *Bernaya (Protocypraea) mississippiensis* sp. nov., holotype, USNM 446797, from MGS loc. 129, ×2.5. Figures 29, 30. *Bernaya (Protocypraea) rineyi* sp. nov., holotype, SDSNH 34008, from SDSNH loc. 3392, ×3.9. Figures 31, 32. *Eocypraea (Eocypraea) louellae* sp. nov., holotype, LACMIP 8281, from LACMIP loc. 28757, ×3.0. Figures 33, 34. *Eocypraea (Eocypraea) mortoni* (Gabb, 1860), holotype, ANSP 13535, from Prairie Bluff, Alabama, ×2.0.

Group, southern India, but differs from the latter by its highly inflated posterior columella, coarser denticulation, less sinuous aperture, and larger size.

Discussion: Good preservation of the holotype permits unequivocal generic and subgeneric assignments. *Eocypraea* **louellae** differs from all other Cretaceous cypraeaceans of North America, and is the earliest known ovulid from the Western Hemisphere.

Material: This species is represented by the well preserved holotype that displays original shell material. A second specimen from the Upper Cretaceous (Cenomanian to Turonian) Hornbrook Formation of Jackson County, Oregon, UCLA loc. 7288, is an internal mold with minor amounts of original shell material.

Type material: Holotype LACMIP 8281. The holotype measures 15.5 mm in length, 12.3 mm in width, and 9.7 mm in height.

Type locality: LACMIP loc. 28757, Putah Creek area of Thompson Canyon, Yolo County, northern California. Upper Cretaceous (Turonian), Yolo Formation.

Etymology: This species is named for LouElla R. Saul (LACMIP) in recognition of her numerous important contributions to Cretaceous and Tertiary molluscan paleontology.

Eocypraea (*Eocypraea*) *mortoni* (Gabb, 1860)

(Figures 33, 34)

C.[*ypraea*] *mortoni* GABB, 1860:391, pl. 68, fig. 9 [not fig. 8].
Cypraea mortoni Gabb, 1860: GABB, 1861:104 [in part]; MEEK, 1864:19 [in part]; WELLER, 1907:722 [in part]; WHITNEY, 1928:154 [in part]; RICHARDS, 1968:162.
Eocypraea (*Eocypraea*) *mortoni* (Gabb, 1860): SCHILDER, 1932: 213; SCHILDER, 1941:102; SCHILDER & SCHILDER, 1971: 67, 135.

Type material: Holotype, ANSP 13535. The holotype measures 17.4 mm in length, 13.9 mm in width, and 11.9 mm in height.

Type locality: Prairie Bluff, Wilcox County, Alabama. Upper Cretaceous (Maastrichtian), Prairie Bluff Formation.

Remarks: *Eocypraea mortoni* is represented by a single poorly preserved internal mold that displays few identifiable shell characters. Schilder (1932) separated material from Prairie Bluff, Alabama, and Burlington County, New Jersey, assigning those from New Jersey to *Palaeocypraea burlingtonensis*. *Eocypraea mortoni* is more globose than *Bernaya* (*Protocypraea*) *burlingtonensis*.

ACKNOWLEDGMENTS

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APPENDIX

Localities Cited

CAS loc. 1345, Texas Springs, 3.2 km E of Horsetown on road leading to Centerville, SW side of road, SW ¼ sec. 28, T31N, R5W, MDBM, Redding Quad, Shasta Co., Calif. Coll.: F. M. Anderson. Lower Cretaceous (Albian), Budden Canyon Formation.

CAS loc. 31918, Thompson Creek, 182.9 m W and 365.8 m N of SE ¼ sec. 20, T8N, R2W, MDBM, Monticello Dam Quad, Yolo Co., Calif. Coll.: W. E. Kennett, 1943. Just above base of Upper Cretaceous (Turonian), Yolo Formation.

CAS loc. 61856 (*ex* CAS loc. 445-A), Fitch Ranch, 3.2 km W of Phoenix, 0.8 km S of Fitch's house, Medford Quad, Jackson Co., Oregon. Upper Cretaceous (Cenomanian/Turonian), Blue Gulch Member, Hornbrook Formation.

CAS loc. 61918 (*ex* S. G. Clark loc. 251), near Gualala, sec. 27(?), T11N, R15W, MDBM, Gualala Quad, Mendocino Co., Calif. Coll.: S. G. Clark. Upper Cretaceous (Maastrichtian), Gualala Group.

LACMIP loc. 28757, Thompson Creek, 640.5 m E of Napa-Yolo Co. line, 823.5 m N of Putah Creek, near mouth of small E flowing ravine, SE ¼ SE ¼ sec. 20, T8N, R2W, MDBM, Monticello Dam Quad, Yolo Co., Calif. Coll.: P. W. Reinhart. Upper Cretaceous (Turonian), Yolo Formation, 3425 m below top of exposed Chico Formation.

LACMIP loc. 10903 (*ex* CIT loc. 1622), near Ashland, along irrigation ditch 45.7–61 m above and to the SW of the Southern Pacific RR tracks at a point 6.43 km SE of U.S. Highway 99 bridge over Ashland Creek, Ashland, Jackson Co., Oregon, near midpoint of W boundary sec. 24, T39S, R1E, WBM, Medford Quad, Oregon. Coll.: W. P. Popenoe and W. A. Findlay, September 1933. Upper Cretaceous (Turonian), Hornbrook Formation.

MGS loc. 129, Chapelville area, 1464 m NE of town on State Highway 348, NE ¼ NE ¼ sec. 29, T7S, R7E, CBM, Ratliff Quad, Lee Co., Miss. Coll.: D. T. Dockery III. Upper Cretaceous (Campanian), "Chapelville fossiliferous horizon" within the Tupelo Tounge sequence of the Coffee Formation.

SDSNH loc. 3162, Carlsbad area, locality (now covered by Faraday Avenue) was exposed during development of Carlsbad Research Center, SW of El Camino Real, S of Letterbox Canyon and N of Palomar Airport, 33°08′02″N, 117°16′41″W, San Luis Rey Quad, San Diego Co., Calif. Coll.: B. O. Riney, T. A. Demére, and M. A. Roeder, March–May 1982. Upper Cretaceous (Campanian/Maastrichtian), Point Loma Formation.

SDSNH loc. 3162-A, Carlsbad area, at the base of stratigraphic section measured at SDSNH loc. 3162, approximately 6.1 m below a calcareous marker bed. Coll.: B. O. Riney, T. A. Demére, and M. A. Roeder, March–May 1982. Upper Cretaceous (Campanian/Maastrichtian), Point Loma Formation.

SDSNH loc. 3162-B, Carlsbad area, 2.1–3.9 m below a calcareous marker bed in measured stratigraphic section at SDSNH loc. 3162. Coll.: B. O. Riney, T. A. Demére, and M. A. Roeder, March–May 1982. Upper Creta-

ceous (Campanian/Maastrichtian), Point Loma Formation.

SDSNH loc. 3162-M, Carlsbad area, near top of exposed stratigraphic section measured at SDSNH loc. 3162. Coll.: B. O. Riney, T. A. Deméré, and M. A. Roeder. Upper Cretaceous (Campamian/Maastrichtian), Point Loma Formation.

SDSNH loc. 3392, Carlsbad area, N of Palomar Airport, roadcut along W side of College Blvd., approximately 424 m S of intersection with El Camino Real, 33°08′21″N, 117°17′02″W, San Luis Rey Quad, San Diego Co., Calif. Coll.: SDSNH field party May 1987. Upper Cretaceous (Campanian/Maastrichtian), Point Loma Formation.

SDSNH loc. 3405, Carlsbad area, N of Palomar Airport, excavation for College Blvd., approximately 242–485 m S of intersection with El Camino Real, 33°08′21″N, 117°17′02″W, San Luis Rey Quad, San Diego Co., Calif. Coll.: B. O. Riney, M. A. Roeder, and R. Q. Gutzler, April–May 1987. Upper Cretaceous (Campanian/Maastrichtian), Point Loma Formation.

SDSNH loc. 3454, Carlsbad area, N of Palomar airport, excavation for College Blvd., approximately 153 m N of College Blvd. and Faraday Ave. intersection, 33°08′11″N, 117°17′02″W, San Luis Rey Quad, San Diego Co., Calif. Coll.: B. O. Riney and M. A. Roeder, April–May 1987. Upper Cretaceous (Campanian/Maastrichtian), Point Loma Formation.

UCLA loc. 7288, Bellinger Hill area, large block displaced to S side of Bellinger Lane and about 0.19 km E of crest of Bellinger Hill by road improvement, approximately 793 m N and 884 m E of NE corner sec. 5, T38S, R2W, in parcel 92, T37S, R2W, WBM, Medford Quad, Jackson Co.. Oregon. Coll.: W. P. Popenoe, R. B. Saul, L. R. Saul, R. B. Saul, and R. L. Saul, 17 June and 23 August 1975. Upper Cretaceous (Cenomanian), Osburger Gulch Sandstone Member, Hornbrook Formation.

USGS loc. 518, bank of Postoak Creek at N edge of Corsicana, Navarro Co., Texas: approximately same as USGS loc. 17012. Coll.: C. A. White and C. B. Boyle, 1890; G. Scott, 1935. Upper Cretaceous (Maastrichtian), Nacatoch Sand, Navarro Group.

USGS loc. 761, near Kaufman on W facing slope of Kings Creek valley, 0.8 km from courthouse where wagon road goes down to Kings Creek, and along E side of creek for 4.8 km S of Kaufman, Kaufman Co., Texas; approximately same as USGS loc. 7545. Coll.: T. W. Stanton, 1890; L. W. Stephenson, 1911. Upper Cretaceous (Maastrichtian), Nacatoch Sand, Navarro Group.

USGS loc. 17702, S side of Chesapeake and Delaware Canal, 91.5 m W of Conrail's Chesapeake and Delaware Canal bridge, northern Delaware. Coll.: C. W. Carter, 1935–37. Upper Cretaceous (Campanian), Marshalltown Formation.

New Paleogene Siliquariid and Vermetid Gastropods from the Pacific Coast of Southwestern North America

by

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Abstract. Two new species of the siliquariid gastropod *Tenagodus* and one new species of the vermetid gastropod *?Serpulorbis* are described from Paleogene strata along the Pacific coast of southwestern North America. The new species of *Tenagodus* are the first reports of this genus from the Pacific coast of North America. The new species of *?Serpulorbis* is the earliest occurrence of a vermetid from the Pacific coast of North America.

Tenagodus californiensis sp. nov. is from outer shelf siltstone in the upper Paleocene Coal Canyon Formation, Santa Monica Mountains, and from similar deposits in the upper Paleocene Santa Susana Formation, Simi Hills, southern California. This new species is the earliest occurrence of *Tenagodus* in North America. *Tenagodus bajaensis* sp. nov. is from inner shelf sandstone in the lower Eocene part of the Bateque Formation, Baja California Sur, Mexico. *?Serpulorbis llajasensis* sp. nov. is from shelf-break glauconitic sandstone in the lower middle Eocene part of the Llajas Formation, Simi Valley, southern California.

INTRODUCTION

Previously, there have been no confirmed reports of siliquariid or vermetid gastropods in the Paleogene fossil record of the Pacific coast of North America. Identification of these gastropods requires inspection of the entire individual or colony (KEEN, 1961), but they are not easily collected as complete specimens. This is especially true when they are in well-indurated rocks like those prevalent in Paleogene deposits of the Pacific coast of North America. Most specimens are collected as fragments and then, understandably, considered by workers to be unidentifiable calcareous tubes formed by tubicolous annelids, and not worthy of systematic treatment. Discovery of nearly complete siliquariid and vermetid specimens in well-indurated Paleogene deposits of southern California and Baja California Sur, Mexico (Figure 1), therefore, is especially noteworthy.

Abbreviations used for catalog and/or locality numbers are as follows: CSUN, California State University, Northridge; IGM, Instituto de Geología, Universidad Nacional Autónoma Museum de México; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; UCLA, University of California, Los Angeles (collections now housed at LACMIP).

MATERIALS

About 60 specimens of *Tenagodus californiensis* sp. nov. were found in the Coal Canyon Formation at locality UCLA 7108 (=locality CSUN 354). This locality is on the west side of the south fork of Garapito Creek at 1200 ft elevation (366 m), 436 m (1430 ft) south and 68.5 m (225 ft) east of the northeast corner of section 5 (projected), T1S, R16W, San Vicente y Santa Monica Grant, Topanga quadrangle (7.5 minute), 1952, photorevised 1967, Santa Monica Mountains, Los Angeles County, southern California. A detailed index map of this locality is given in SQUIRES (1980).

Three specimens of *Tenagodus californiensis* were also found in the lower middle part of the Santa Susana Formation at locality CSUN 1290. This locality is on the east side of Bus Canyon at 1250 ft elevation (381 m), 381 m (1250 ft) north and 372 m (1220 ft) west of the southeast corner of section 28, T2N, R18W, Thousand Oaks quadrangle (7.5 minute), 1950, photorevised 1967, Simi Hills, Ventura County, southern California.

Three specimens of *Tenagodus bajaensis* sp. nov. were found in the Bateque Formation at locality CSUN 1291a. This locality is on the south side of a minor canyon near the southern end of Mesa La Salina at 120 m elevation,

at 112°56′13″W and 26°40′N, San Jose de Gracia quadrangle (1:50,000), number G12A64, 1983, Baja California Sur, Mexico.

Five specimens of *?Serpulorbis llajasensis* sp. nov. were found in the LACMIP collections of the "Stewart bed" that crops out near the middle of the Llajas Formation at locality UCLA 2313 (=locality CSUN 374). This locality, which is in a tributary to Las Llajas Canyon, is at elevation of 1700 ft (518 m) on a small cliff on the south side of a side canyon, 594 m (1950 ft) north and 556 m (1825 ft) east of the southeast corner of section 29, T3N, R17W, Santa Susana quadrangle (7.5 minute), 1951, photorevised 1969, northern Simi Valley, Ventura County, southern California. A detailed index map of this locality is given in Squires (1983, 1984).

DEPOSITIONAL ENVIRONMENTS AND GEOLOGIC AGES

The abundant specimens of *Tenagodus californiensis* in the Coal Canyon Formation at locality UCLA 7108 were found as an intergrown mass in a concretion within siltstone. Associated macrofauna, which was described by Squires (1980), is sparse and includes several genera of bivalves and gastropods, and one genus each of heart urchin and crab. Neither the intergrown mass of *Tenagodus* nor the associated macrofauna show signs of abrasion due to post-mortem transport, and they were interpreted by Squires (1980) to be *in situ* in a shallow subtidal environment that would be equivalent to the outer shelf environment as defined by Bottjer & Jablonski (1988). Squires (1980) reported the deposits at this locality to be late Paleocene in age. The common presence of *Turritella infragranulata* Gabb, 1864, at this locality is further evidence of such an age because this turritellid is probably indicative of the upper middle to upper Thanetian Stage (late Paleocene) (Saul, 1983).

The few specimens of *Tenagodus californiensis* in the Santa Susana Formation at locality CSUN 1290 were found as isolated but nearly complete individuals within a 2.5-m-thick muddy siltstone unit interbedded within a more sparsely fossiliferous very fine-grained sandstone sequence. Associated macrofauna is uncommon and included several genera of infaunal bivalves, two genera of terebratulid brachiopods, and two genera of gastropods. The bivalves and brachiopods are articulated and some show growth series. No suitable hard substrate was found that could have provided attachment for the brachiopods and the specimens of *Tenagodus*. Unlike the bivalves, the brachiopods may have been transported, but the amount of post-mortem transport was not great because indications of significant abrasion were absent. The specimens of *Tenagodus* may have undergone a similar amount of post-mortem transport, or they may be essentially *in situ* if they had lived embedded in sponges like certain modern species of *Tenagodus* that have been reported (Morton, 1955; Gould, 1966; R. Bieler, personal communication) in the
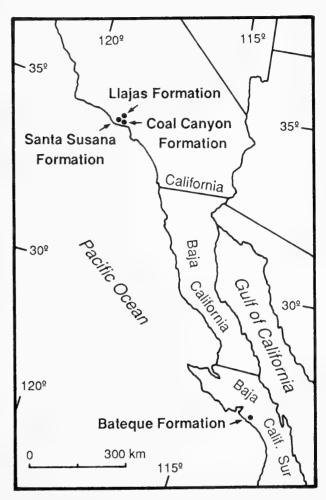
Figure 1

Stratigraphic occurrences of the new Paleogene siliquariid and vermetid gastropods.

western Atlantic. The deposits at locality 1290 plot on Parker's (1983:figs. 4, 6) measured section A of the Santa Susana Formation in Bus Canyon at about 600 m above the base of the underlying Simi Conglomerate. Parker (1983) interpreted this part of the Santa Susana Formation to have been deposited in an offshore shelf environment that would be equivalent to outer shelf deposits as defined by Bottjer & Jablonski (1988). This part of the Santa Susana Formation is correlative to the upper Paleocene Thanetian Stage based on the presence of calcareous nannofossils found by Filewicz & Hill (1983) and planktonic foraminifera found by Heitman (1983). Age-diagnostic macrofossils at locality 1290 are the bivalve *Pholadomya* (*Bucardiomya*) *mounti* Zinsmeister and the gastropod *Fulgoraria* (*Psephaea*) *zinsmeisteri* Mount. Zinsmeister (1983) reported these species from upper Paleocene strata elsewhere in the Santa Susana Formation, Simi Hills.

The few specimens of *Tenagodus bajaensis* in the Ba-

teque Formation at locality 1291a were found as isolated but mostly complete individuals in a lens consisting of fossiliferous very fine-grained sandstone surrounded by bioturbated very fine-grained sandstone. Associated macrofauna included several genera of gastropods, and one genus each of scaphopod and solitary scleractinian coral. In addition, abundant fragments of discocyclinid foraminifera were present. The lens represents a concentration of fossil material, much of which is fragmental. This *Tenagodus*-bearing lens is interpreted to be a storm deposit in an inner shelf environment, as defined by BOTTJER & JABLONSKI (1988). The amount of post-mortem transport of the larger fossils, like the specimens of *Tenagodus,* however, was not great because the amount of abrasion is low. Lithologically and paleontologically, the deposits at locality 1291a are similar to exposures of the Bateque Formation about 10 km to the north at locality CSUN 1220b. Geologic details of that particular locality are given in SQUIRES & DEMETRION (1990), who reported that the deposits at locality 1220b are correlative to the lower Eocene Ypresian Stage based on the presence of planktonic foraminifera.

The rare specimens of *?Serpulorbis llajasensis* in the Llajas Formation at locality UCLA 2312 were found in the 1-m-thick silty glauconitic sandstone of the "Stewart bed." The rocks at this locality are richly fossiliferous and have been the subject of extensive macropaleontologic work by SQUIRES (1983, 1984). The "Stewart bed" represents an *Eocernina-Turritella-Crassatella-?Trochocyathus* paleocommunity with at least 50 species of macrofossils that lived near the shelf-slope break (SQUIRES, 1984). The bed, which is 355 m above the base of the formation, is correlative to the middle Eocene Lutetian Stage based on the presence of calcareous nannofossils found by FILEWICZ & HILL (1983).

SYSTEMATIC PALEONTOLOGY

Superfamily CERITHIODEA Fleming, 1822

Family SILIQUARIIDAE Anton, 1838

Genus *Tenagodus* Guettard, 1770

Type species: By subsequent designation (SACCO, 1896), *Serpula anguina* Linné, 1758, Recent, Indian Ocean.

Discussion: As mentioned in GOULD (1966), older classifications placed all irregularly coiled mesogastropods in the family Vermetidae, but MORTON (1951) removed the Siliquariidae from this vermetid complex. R. Bieler (personal communication), who is currently reviewing the anatomy and biology of certain members of the siliquariids, now recognizes two groups in this family: namely, those with a slit (*Tenagodus* and *Pyxipoma*) and those without a slit (*Stephopoma*).

GOULD (1966) stated that because GUETTARD (1770) used a nonbinomial designation for the type species in naming *Tenagodus,* the name is invalid and *Siliquaria* Bruguière, 1789, should be used instead. However, according to ICZN Article 11(c)(i), the binomial form of LINNÉ (1758) is not required in the formation of a genus name in works published before 1931; hence, the name *Tenagodus* is valid.

WENZ (1939) and DAVIES (1971) reported the geologic range of *Tenagodus* as Middle Triassic to Recent.

Tenagodus californiensis Squires, sp. nov.

(Figures 2–5)

Diagnosis: A *Tenagodus* with about 14 coarse spiral ribs on outer side of each whorl and about 10 fine spiral ribs on inner side of each whorl.

Description: Shell medium size, up to 65 mm length (incomplete) and 6.5 mm width (incomplete). Solitary or colonially intergrown. Protoconch missing. Loosely spirally coiled in juvenile stage, irregular to tubelike in later stages. Shell with about 14 slightly beaded coarse spiral ribs on outer side of each whorl, coarsest at maximum curvature of outer side, and about 10 fine spiral ribs on inner side of each whorl. Interspaces between coarse spiral ribs rarely with one secondary spiral rib. In some specimens, spiral ribs on inner side of each whorl also coarse. Longitudinal slit in posterior part of each whorl, usually open in juvenile stage but commonly filled in later stages and forming angulation on tube.

Discussion: *Tenagodus californiensis* is most similar to *T. (Agathirses) striatus* (DEFRANCE, 1827:214; DESHAYES, 1861:292, pl. 10, figs. 7, 14; COSSMANN & PISSARRO, 1910–1913:pl. 22, fig. 132-1; COSSMANN, 1912:147, pl. 10, fig.

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Explanation of Figures 2 to 10

Figures 2 to 5. *Tenagodus californiensis* sp. nov. Figure 2. Holotype, LACMIP 8086, internal mold, lateral view, locality CSUN 1290, ×1.7. Figures 3 and 4. Paratype, LACMIP 8087, locality UCLA 7108, ×3. Figure 3. Oblique dorsal view. Figure 4. Lateral view. Figure 5. Paratype, LACMIP 8088, lateral view of inner side of whorl, locality UCLA 7108, ×3.

Figures 6 to 8. *Tenagodus bajaensis* sp. nov., locality CSUN 1291a. Figure 6. Holotype, IGM 5102 = plastoholotype, LACMIP 8089, lateral view, ×2.6. Figures 7 and 8. Paratype, IGM

5103 = plastoparatype, LACMIP 8090. Figure 7. Lateral view, ×1.4. Figure 8. Oblique dorsal view of same specimen shown in Figure 7 but with the upper spire whorls removed to expose the longitudinal slit, ×1.8.

Figures 9 and 10. *?Serpulorbis llajasensis* sp. nov., locality UCLA 2312. Figure 9. Holotype, LACMIP 8091, lateral view of three weathered colonial specimens, ×3. Figure 10. Paratype, LACMIP 8092, lateral view, ×3.

16; GLIBERT, 1933:49, pl. 3, fig. 4) from middle Eocene (Lutetian Stage) strata of the Paris Basin, France. A comparison of *T. californiensis* with four UCMP Cloez collection specimens of *T. (A.) striatus* from Chaussy, Oise, Paris Basin and with three specimens of *T. (A.) striatus* collected by the author from Villiers-St.-Frederic, Paris Basin, revealed that *T. californiensis* differs in the following features: presence of numerous fine spiral ribs on the inner side of each whorl rather than being smooth, ribs are coarser and more closely spaced on outer side of each, much less development of a secondary spiral rib in the interspaces, a slit that becomes partly filled rather than remaining open throughout growth, and no development of cancellate ornamentation.

Tenagodus californiensis and the slightly younger *T. bajaensis* are the first reports of this genus from the Pacific coast of North America. The only other Paleogene species of *Tenagodus* known from North America are two species from upper middle Eocene strata in the southeastern United States (PALMER & BRANN, 1966; TOULMIN, 1977). Neither is similar to the new species.

Etymology: The specific name is for California.

Material: About 63 specimens, 60 of which were an intergrown mass. The other three are solitary forms.

Occurrence: Upper Paleocene Thanetian Stage. Coal Canyon Formation, Santa Monica Mountains, southern California, locality UCLA 7108; lower middle Santa Susana Formation, Simi Hills, southern California, locality CSUN 1290.

Repository: Holotype, LACMIP 8086, locality CSUN 1290; paratypes, LACMIP 8087 to 8088, locality UCLA 7108.

Tenagodus bajaensis Squires, sp. nov.

(Figures 6–8)

Diagnosis: A *Tenagodus* with scaly looking, fairly low but elongate hollow spines.

Description: Shell medium size, up to 52 mm length (incomplete) and 10 mm width (incomplete). Solitary. Protoconch missing. Loosely spirally coiled in juvenile stage, irregular in later stages. Outer side of each whorl with about 6 strong spiral ribs with scaly looking, fairly low but elongate hollow spines which, when eroded down to base, form horizontal "V" shape with point of "V" directed adapically. Fairly wide interspaces between ribs. Longitudinal slit in posterior part of each whorl and open throughout; possible row of holes in slit in juvenile stage.

Discussion: *Tenagodus bajaensis* is similar to *T. (Agathirses) faujasi* (DESHAYES, 1861:290, pl. 10, figs. 3–4; COSSMANN & PISSARRO, 1910–1913:pl. 22, fig. 132-3) from middle Eocene (Lutetian Stage) strata of the Paris Basin, France. A comparison between *T. bajaensis* and two

UCMP Cloez collection specimens of *T. (A.) faujasi* from Chaussy, Paris Basin, revealed that *T. bajaensis* differs in the following features: spines are coarser, more laterally elongate, not as projecting (especially on ventral side of each whorl), and have a much more overlapping scaly look.

Etymology: The specific name is for the peninsula of Baja California, Mexico.

Material: Three solitary specimens.

Occurrence: Lower Eocene, Ypresian Stage. Bateque Formation, Baja California Sur, Mexico, locality CSUN 1291a.

Repository: Holotype, IGM 5102 = plastoholotype, LACMIP 8089; paratype, IGM 5103 = plastoparatype, LACMIP 8090, locality CSUN 1291a.

Superfamily VERMETOIDEA Rafinesque, 1815

Family VERMETIDAE Rafinesque, 1815

Genus *Serpulorbis* Sassi, 1827

Type species: By monotypy, *Serpulorbis polyphragma* Sassi, 1827, Recent, Mediterranean Sea.

Discussion: Recent research by HEALY (1988) on sperm structure indicates a separate superfamily Vermetoidea for the family Vermetidae.

As fossil material, the only morphologic distinction between the genera *Serpulorbis* and *Vermetus* Daudin, 1800, is that *Serpulorbis* has no operculum whereas *Vermetus* has a corneous one. Unfortunately, corneous material is rarely preserved in the fossil record. Currently, the only criterion available to distinguish these two genera is the rather dubious one of geologic age range. WENZ (1939), KEEN (1961), and DAVIES (1971) reported the geologic range of *Serpulorbis* to be Upper Cretaceous?, Eocene to Recent. GARDNER (1933) and PALMER & BRANN (1966), however, reported lower and upper Paleocene species. WENZ (1939) and DAVIES (1971) reported the geologic range of *Vermetus* to be Pliocene to Recent. SMITH (1986), however, reported a middle Miocene species.

?*Serpulorbis llajasensis* Squires, sp. nov.

(Figures 9, 10)

Diagnosis: A *Serpulorbis*-like vermetid with noded cancellate ornamentation in which the collabral costae are the same strength as the spiral ribs.

Description: Shell small size, up to 28 mm length (incomplete) and 3.5 mm width (incomplete). Solitary or colonially intergrown. Protoconch missing. Loosely spirally coiled in early juvenile stage, tubelike in later stages. Shell covered with closely spaced (1 every mm) prominent collabral costae, nodose where intersecting 10 equal-strength spiral ribs covering the shell, producing cancellate

ornamentation. One (rarely 2) secondary riblets sometimes in interspaces.

Discussion: Although a protoconch appears to be present in the lowermost individual of the holotype, LACMIP 8091 (Figure 9), the dome-shaped structure is only the result of weathering in the apical area.

?Serpulorbis llajasensis is similar to *S. polygonus* DESHAYES (1861:285, pl. 9, fig. 14; COSSMANN & PISSARRO, 1910–1913:pl. 22, fig. 131-12) from lower through upper Eocene (Ypresian Stage through Bartonian Stage) strata in Paris Basin, France. A comparison between *?S. llajasensis* and eight UCMP Cloez collection specimens of *S. polygonus* from Crenes, Oise, Paris Basin, revealed that *?S. llajasensis* differs in the following feature: cancellate ornamentation is much more developed because the collabral costae and spiral ribs are nearly equal rather than having weaker collabral costae.

Whether or not the new species possesses an operculum is not known, and thus a definite generic assignment cannot be made. The new species is questionably assigned to *?Serpulorbis* because the geologic range of this genus, unlike *Vermetus,* encompasses the middle Eocene age of the new species. *?Serpulorbis* is known from lower Paleocene, upper Paleocene, and upper Eocene strata in the eastern United States (GARDNER, 1933; PALMER & BRANN, 1966; TOULMIN, 1977), but previously the genus has not been reported from the Paleogene of the Pacific coast of North America. It is only known from the Pleistocene to Recent in this particular area (GRANT & GALE, 1931; KEEN, 1961). The new species is not like any of the other fossil or Recent *Serpulorbis* from North America. The new species is also not like any fossil or Recent *Vermetus* from North America. *?Serpulorbis llajasensis* is the earliest occurrence of a vermetid from the Pacific coast of North America.

Etymology: The specific name is for the Llajas Formation.

Material: Five specimens, three of which are intergrown. The other two are solitary forms.

Occurrence: Middle Eocene Lutetian Stage. Middle Llajas Formation, northern Simi Valley, southern California, locality UCLA 2312.

Repository: Holotype, LACMIP 8091, and paratype, LACMIP 8092; locality UCLA 2312.

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Tibiaporrhais, a New Late Cretaceous Genus of Aporrhaidae Resembling *Tibia* Röding

by

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Abstract. Newly discovered late Campanian specimens of the gastropod ?*Nudivagus cooperensis* Stephenson, 1941, reveal a spined outer lip characteristic of the Aporrhaidae. This feature necessitates removal of this species from the Cerithiidae and placement in a new genus, *Tibiaporrhais*, of the Aporrhaidae. The type species of *Nudivagus*, *N. simplicus* Wade, 1917, lacks evidence of an aporrhaid aperture and is retained in the Cerithiidae because of this and other differences in shell morphology that separate it from ?*Nudivagus cooperensis*. Unfortunately, a complete aperture for the type species of *Nudivagus* is unknown; *Nudivagus* therefore cannot be absolutely precluded from the Aporrhaidae.

Tibia japonica (Nagao, 1932), from the Campanian of Soviet Sakhalin, also is placed in *Tibiaporrhais* gen. nov., as is a similar undescribed species from the Campanian of California. Similarities in shell morphology between *Tibiaporrhais* and *Tibia* Röding, 1798, suggest either a relatively close evolutionary relationship between the genera, implying that *Tibia* may be more closely allied to the Aporrhaidae than to the Strombidae, or that the genera are homeomorphic. Anatomical research is needed in order to assess these possibilities.

INTRODUCTION

The classification of fossil gastropods lacking ornament is often a difficult and confusing task, especially when the easily damaged apertures are usually incomplete. This problem is especially evident in the case of the Late Cretaceous ?*Nudivagus cooperensis,* which was known for over 40 yr before newly discovered specimens with nearly complete apertures indicated the need for placement in a new genus of the Aporrhaidae.

This paper will name and document *Tibiaporrhais,* the new genus of the Aporrhaidae, and further describe and illustrate *Tibiaporrhais cooperensis* (Stephenson, 1941), the type species. In addition to this late Campanian to early Maastrichtian species of the Western Interior and Gulf Coast of North America, two Campanian north Pacific species, *Tibia japonica* (Nagao, 1932) and a newly discovered species from California, will be assigned to *Tibiaporrhais*. These latter species may provide ancestors to the present day Indo-Pacific *Tibia*.

SYSTEMATIC PALEONTOLOGY

The specimens described or mentioned in this paper have the following repository or locality (loc.) abbreviations: USNM—National Museum of Natural History (formerly United States National Museum); UCM—University of Colorado Museum, Boulder, Colorado; USGS—U.S. Geological Survey; CAS—California Academy of Sciences.
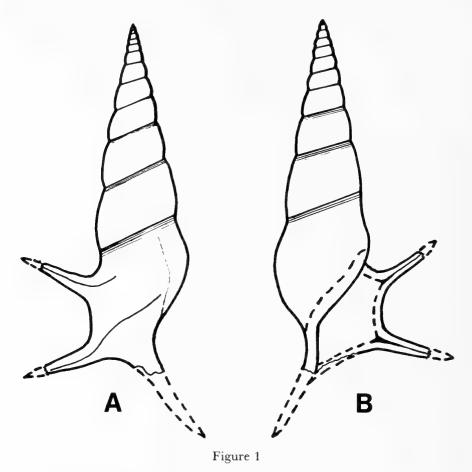
Family APORRHAIDAE Mörch, 1852

Genus *Tibiaporrhais* Elder, gen. nov.

(Figures 1, 3, 4, 6–9)

Type species: ?*Nudivagus cooperensis* Stephenson, 1941, here designated.

Diagnosis: A large, high spired aporrhaid having (1) subdued sculpture consisting of fine spiral striae and growth lines, and (2) a slightly expanded outer lip with two, moderately long, spinelike processes that arise from indistinct carinae that extend for less than the latter half of the body whorl.

Description: Shell large for family (8 to 10 cm in length); turriculate, having 8 to 11 whorls and spire angle of 20 to 30 degrees. Whorl sides broadly convex anteriorly and slightly constricted posteriorly below a distinct, but closely appressed suture. Surface ornament weak; consisting of numerous crowded, narrow spiral striae and fine, sinuous axial growth lines. Aperture moderately elongate and trap-

Figure 1

Reconstruction of *Tibiaporrhais* cooperensis (Stephenson, 1941) based on a composite of three specimens, ×1. A, abapertural view; B, apertural view. Dashed lines denote portions of shell not present on any specimen and therefore subjectively drawn.
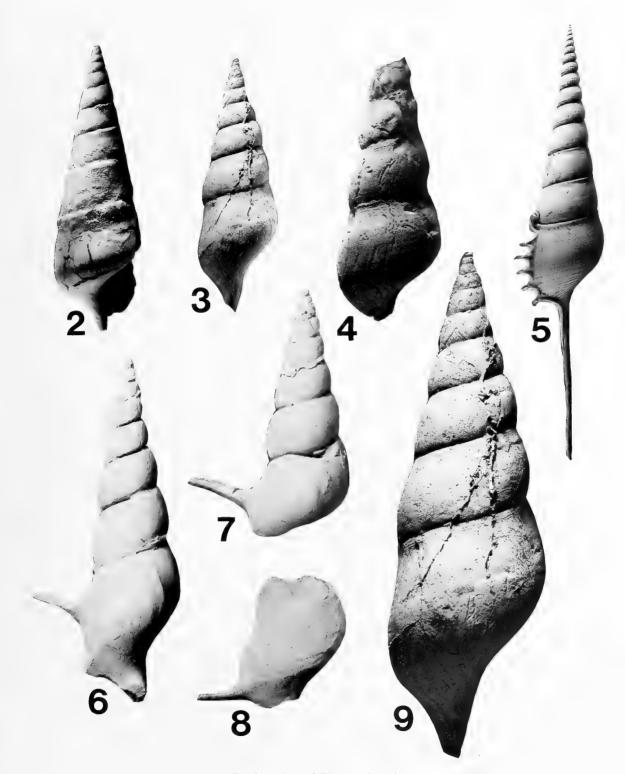
ezoidal. Outer lip slightly flaring with two discrete spine-like processes originating from two indistinct carinae that extend for less than one-third of body whorl; posterior process projects in slightly posterior direction, anterior process projects in horizontal to slightly anterior direction. Anterior canal broken on all specimens, but suggestive of moderate length (Figure 1). Inner lip slightly callused. Lacks evidence of posterior canal or callus extending upwards onto spire.

Remarks: This genus is most similar to *Dicroloma* Gabb, 1868, but differs significantly in lacking carinae on the spire. *Tibiaporrhais* also is similar to *Lispodesthes* White, 1875, but has a higher spire and lacks secondary callus. The new genus differs significantly from *Aporrhais* DaCosta, 1778, *Tessarolax* Gabb, 1864, and *Helicaulax* Gabb, 1868, in not possessing a posterior canal attached to the spire by callus, and from *Gymnarus* Gabb, 1868, *Pyktes* Popenoe, 1983, and *Tephlon* Popenoe, 1983, by having a higher spire, and by lacking secondary callus and a heavy, bent, posterior projection of the outer lip. *Tibiaporrhais* differs from *Anchura* Conrad, 1860, by lacking

the broadly flaring outer lip with posteriorly projecting process characteristic of the latter genus. The lack of both a broadly flaring outer lip and prominent surface ornament, as well as the presence of two discrete lateral spines, serve to distinguish *Tibiaporrhais* from *Drepanochilus* Meek, 1864, *Arrhoges* Gabb, 1868, and *Graciliala* Sohl, 1960.

Tibiaporrhais apparently includes not only the late Campanian to early Maastrichtian species ?*Nudivagus cooperensis,* but also the Campanian species *Tibia japonica* (Nagao, 1932) from Sakhalin. The surface ornament and constriction below the suture are slightly stronger on the latter species than the former (for comparison see NAGAO, 1932:44–45, pl. 7, figs. 1–3, 5, 6; HAYAMI & KASE, 1977: 59, pl. 7, fig. 4), but their overall shape, size, and ornamentation are very similar. The apertures of all *Tibia japonica* specimens are imperfect, but NAGAO (1932) states that the thin outer lip bears two processes of unknown length that originate from relatively indistinct carinae on the body whorl (see NAGAO, 1932:pl. 7, fig. 3b). In addition, a specimen from Campanian strata in the Sacramento Valley of California (Figure 4) bears strong resem-

Explanation of Figures 2 to 9

Figure 2. *Nudivagus simplicus* Wade, 1917; Holotype, USNM 32938, ×1. Figure 3. ***Tibiaporrhais*** *cooperensis* (Stephenson, 1941); UCM 30670, latex peel of external mold, ×1. Figure 4. ***Tibiaporrhais*** sp.; USNM 442113, ×1. Figure 5. *Tibia fusus* Linné, 1758; CAS 66959, ×0.5. Figures 6–9. ***Tibiaporrhais*** *cooperensis* (Stephenson, 1941); UCM 30670. Figures 6, 7. Internal molds with posterior spinelike process intact, ×1. Figure 8. Internal mold with anterior spinelike process intact, ×1. Figure 9. Latex peel of external mold showing fine ornamentation of shell-surface, ×2.

blance to **Tibiaporrhais** *japonica* (Nagao, 1932) and also is tentatively placed in **Tibiaporrhais**, despite its broken aperture that shows no evidence of spinelike processes. Features of this specimen are discussed below.

Nudivagus Wade, 1917, is not reassigned to the Aporrhaidae because evidence for an expanded aperture and apertural spines is lacking in the type species, *Nudivagus simplicus* (Figure 2). In addition, this species has a narrow, tabulate shoulder, flatter whorl sides, and sharper angulation from the anterior to peripheral sides of the body whorl relative to **Tibiaporrhais** *cooperensis* (Figure 3) (for comparison see WADE, 1917, 1926; STEPHENSON, 1941; SOHL, 1960). The shape of the growth lines and the spiral striae constituting the surface ornament of the two species are very similar, however, and incomplete apertures on all specimens of *Nudivagus simplicus* do not absolutely preclude this species from being congeneric with *T. cooperensis*.

Occurrence: **Tibiaporrhais** is known from strata of late Campanian and early Maastrichtian age in the Western Interior and Gulf Coast regions of the United States, respectively. It is also found in Campanian age strata of the eastern North Pacific in central California and of the western North Pacific in Soviet Sakhalin.

Etymology: **Tibiaporrhais**—A *Tibia*-like aporrhaid.

Tibiaporrhais *cooperensis* (Stephenson, 1941)

(Figures 1, 3, 6–9)

?*Nudivagus cooperensis* STEPHENSON, 1941:294–295, pl. 54, figs. 11, 12; SOHL, 1960:79; WOLFE & KIRKLAND, 1986: 207.

Material: Holotype—USNM 76900, USGS collection 14063: one moderately well-preserved specimen with broken aperture and anterior canal. Hypotypes—UCM 30670, loc. 81007: two internal molds with posterior processes preserved and broken anterior canals, one internal mold of body whorl with anterior process preserved, and one well-preserved external mold without aperture or anterior canal.

Description: Shell thin, large, turriculate (preserved portions of adult specimens 75 to 90 mm in height), with 10 to 11 whorls and spiral angle of about 30 degrees (Figures 3, 6). Whorl sides broadly convex and slightly constricted anterior of closely appressed suture. Surface ornament consisting of weak spiral striae and axial growth lines (Figure 9). Spiral striae and interspaces broader and more distinct immediately anterior of suture, becoming narrower, less distinct, and finally disappearing on anterior half of whorls. Sinuous growth lines slightly prosocline below suture, increasing in angle on upper half of whorl, and arching over whorl periphery. Slightly prosocline poorly defined swelling developed one-third revolution back from aperture on external surface of body whorl; swelling well developed on internal mold and accompanied by a slight abapertural

constriction. Ventral periphery of body whorl broadly rounded. Two indistinct carinae present on body whorl behind spinelike lateral labral processes; anterior carinae sinuous at base of process, extending back to vertical swelling; posterior carinae posteriorly bending at base of spine, extending back less than one-quarter revolution (Figure 7). Anterodorsal margin of body whorl sharply constricted between anterior carinae and anterior canal. Length and shape of anterior canal uncertain; available material suggesting a moderately long, ventrally bending, spinelike process (Figure 1). Aperture moderately elongate and trapezoidal, but poorly defined from existing material. Outer lip slightly flaring with two 15 to 18 mm long spinelike processes; posterior spine projecting in posterior direction (ca. 70 degrees from axis of spire) (Figures 6, 7), anterior spine projecting in horizontal to slightly anterior direction (Figure 8). Inner lip slightly callused. Lacks evidence of posterior canal or callus extending upwards onto spire.

Remarks: **Tibiaporrhais** *cooperensis* differs from **Tibiaporrhais** *japonica* (Nagao, 1932) and **Tibiaporrhais** sp. (Figure 4) by having a greater apical angle (ca. 30 degrees versus 20 degrees), greater number of whorls (ca. 11 versus 8), finer and less prominent spiral striae, and less well-developed constriction of the whorl periphery below the suture.

Occurrence: Holotype from the lower Maastrichtian (*Exogyra cancellata* zone) Navarro Group, Neylandville Marl, near Cooper, Texas. Hypotypes from the upper Campanian (upper *Baculites compressum* to lower *Baculites cuneatus* zones), middle part of the Pierre Shale near Kremmling, Colorado (see Appendix for locality descriptions).

Tibiaporrhais sp.

(Figure 4)

Material: Illustrated specimen—USNM 442113, USGS Mesozoic loc. M4013. One moderately preserved specimen with spire, aperture, and anterior canal broken.

Remarks: This specimen strongly resembles **Tibiaporrhais** *japonica* in having a spire with ca. 8 whorls and an apical angle of ca. 20 degrees, and in being more constricted between the suture and whorl periphery than is *T. cooperensis* (compare with NAGAO, 1932:pl. 7, figs. 1, 2; HAYAMI & KASE, 1977:pl. 7, fig. 4). However, the lower whorl periphery is more rounded anteriorly than on *T. japonica,* more closely resembling *T. cooperensis* in this respect. The spiral striae and axial growth lines of **Tibiaporrhais** sp. appear to be intermediate in strength between those of *T. japonica* and *T. cooperensis,* although the worn nature of the shell surface makes this observation somewhat suspect. Overall characteristics of this specimen suggest that it belongs to a species closely allied to *T. japonica* and somewhat intermediate in character between that species and *T. cooperensis*; however, better material is needed before this apparently new species can be adequately described.

Occurrence: Forbes Formation of the Chico "series" (KIRBY, 1943) in the Rumsey Hills, Yolo County, California; from Campanian strata (see Appendix for locality descriptions).

DISCUSSION

The distribution of *Tibiaporrhais* in the North Pacific, Western Interior, and Gulf Coast regions of North America further supports SOHL's (1967, 1971) suggested link between the North Pacific and Western Interior regions during the Late Cretaceous. Based on similarities in the distribution patterns of gastropod genera, particularly between Sakhalin and the Western Interior region (SOHL, 1967), SOHL (1971) hypothesized a northern migration route between the regions or an unknown "boreal" fauna supplying migrants to both regions simultaneously.

In addition, morphological similarities between the shells of *Tibiaporrhais* and the Indo-Pacific genus *Tibia* suggest a possible evolutionary link between these genera; both share the general characteristics of having (1) a high spire, (2) broadly convex whorls, (3) weak sculpture consisting primarily of fine spiral striae and axial growth lines, (4) a moderately flaring lip with digitations, and (5) a long to moderately long anterior siphonal canal that is straight to slightly bent (compare Figures 1 and 5). One notable difference in shell morphology between *Tibiaporrhais* and *Tibia* is the development of the posterior canal and callus on the spire of the latter genus. *Tibiaporrhais* is here placed in the Aporrhaidae based on the aporrhaid characteristics of (1) a high-spired shell having many whorls, (2) the two spinelike processes extending from the outer lip, and (3) the slightly bent, spinelike anterior canal. *Tibia* is presently assigned to the Strombidae, but differs from most strombids in having a higher spire, longer anterior canal, and lacking the "stromboid notch" that allows protrusion of the stalked right eye (ABBOTT, 1960); however, *Tibia* does possess the strombid features of stalked eyes, a hooklike operculum, and a long foot (H. & A. ADAMS, 1853; ABREA, 1975).

With POPENOE's (1983) reassignment of the genus *Pugnellus* Conrad, 1860, from the Strombidae to the Aporrhaidae, the earliest undoubted strombid is of latest Maastrichtian age (POPENOE, 1983). Thus, *Tibia* possibly belongs to a conservative ancestral stock of strombids descending from or of common ancestry with *Tibiaporrhais*, and which split from the main stock of Strombidae at an early point in its radiation. *Tibia* may therefore retain some aporrhaid features while possessing some strombid characters. The ambiguous nature of *Tibia* and its similarity in shell morphology to *Tibiaporrhais* indicate the need for a comparative analysis of the soft-part anatomy of extant *Tibia* and other Strombidae and Aporrhaidae in order to assess properly their evolutionary relationships. Comparative analysis of DNA sequencing in these groups may also shed light on this problem. The results of such studies should determine the family to which *Tibia* is more closely allied, and whether the similarities in shell morphology between *Tibia*

and *Tibiaporrhais* reflect a close evolutionary relationship or merely homeomorphy in genera from two families of Strombacea.

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APPENDIX

Locality Information

USGS Collection 14063. Branch east of Texas Midland Rail Road, 0.4 mi. (0.6 km) N of Cooper, Delta County, Texas. Greenish-gray calcareous clay (marl) with calcium carbonate concretions. Collected by L. W. Stephenson, 1928.

UCM Locality 81007. Near top of S side of prominent SE pointing butte. Grand County, Colorado, Kremmling 1:62,500 Quadrangle, NW¼SE¼SW¼ sec. 7, T3N, R80W. Collected by J. Kirkland, 1981–1982.

USGS Mesozoic Locality M4013. SE side of intermittent creek, S of Petroleum Creek, N of Guinda VABM, Yolo County, California. Rumsey 1:24,000 Quadrangle, 1450 ft. (442 m) E and 2450 ft. (747 m) S of NW corner of sec. 11, T12N, R3W. Collected by E. Pessagno, 1965–1966.

Relocation of *Ervilia* Turton, 1822 (Bivalvia) from the Mesodesmatidae (Mesodesmatoidea) to the Semelidae (Tellinoidea)

by

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Abstract. *Ervilia* Turton, 1822, is represented by a few small tropical and subtropical species. The familial placement of the genus has been in question since its original description. On the basis of hinge and ligament structure, the presence of a posteroventral cruciform muscle in the fused ventral mantle margins, and other anatomical features, *Ervilia* is here relocated from the Mesodesmatidae (Mesodesmatoidea) to the Semelidae (Tellinoidea). We suggest that the Erviliinae Dall, 1895, be abandoned and that the remaining constituent genera, *i.e.*, *Coecella* Gray, 1853, and *Argyrodonax* Dall, 1911, be temporarily relocated in the Mesodesmatinae pending fuller revision of the Mesodesmatidae and Mesodesmatoidea. Lectotypes are designated for *Ervilia nitens* (Montagu, 1808) and *Ervilia castanea* (Montagu, 1803).

INTRODUCTION

According to contemporary authorities (BEU, 1971; SAKURAI & HABE, 1973; VOKES, 1980; BOSS, 1982), the Mesodesmatidae Gray, 1840, comprises three subfamilies: Mesodesmatinae Gray, 1840, Davilinae Dall, 1895, and Erviliinae Dall, 1895. Several representatives of the Mesodesmatinae have received extensive study, *e.g.*, *Mesodesma arctatum* (Conrad, 1830) (ALLEN, 1975) and *M. mactroides* Deshayes, 1854 (NARCHI, 1981). NARCHI (1980) reported on the functional morphology of *Caecella chinensis* Deshayes, 1855 (Erviliinae). YONGE & ALLEN (1985) investigated *M. arctatum*, *Atactodea striata* (Gmelin, 1791) (Mesodesmatinae), *Davila plana* (Hanley, 1843) (Davilinae), and *Ervilia castanea* (Erviliinae) and concluded that they were all similar to each other in terms of ligament structure and collectively different from the Mactridae, such that the Mesodesmatidae Gray, 1840, should be separated from the mactrids and placed in their own superfamily, the Mesodesmatoidea Gray, 1840.

MORTON (in press) and this paper demonstrate significant anatomical differences in *Ervilia castanea* from the mesodesmatoid plan, unnoticed by YONGE & ALLEN (1985). This paper investigates the type material of *Ervilia nitens*, the type species of *Ervilia*, and *E. castanea* and summarizes significant anatomical features of the latter that justify separation of the genus from the Mesodesmatidae. It also examines likely relatives of *Ervilia* and recommends placement in the Semelidae Stoliczka, 1870 (Tellinoidea).

SYSTEMATIC TREATMENT

Designation of Lectotypes

In the recent systematic treatments of *Ervilia* (ROOIJ-SCHUILING, 1972, 1973; DAVIS, 1973; BABIO & BONNIN, 1987) lectotypes were not selected for Montagu's two species of *Ervilia*. To stabilize the taxa treated in this paper, we have selected lectotypes for *Ervilia nitens* and *Ervilia castanea*.
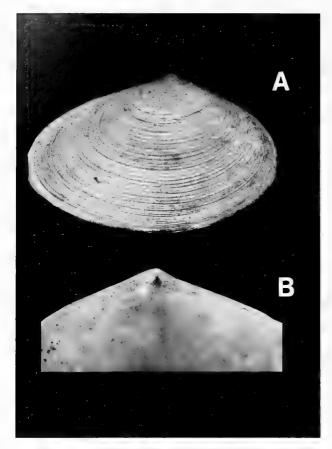
Figure 1

Ervilia nitens (Montagu, 1808); **Lectotype (herein)** of *Mya nitens* Montagu, 1808; right valve, Dunbar, Scotland; Royal Scottish Museum 1866.21a.43. A. Exterior, 7.0 mm length, 4.4 mm height. B. Close-up of hinge.

Ervilia nitens (Montagu, 1808)

(Figure 1)

Mya nitens MONTAGU, 1808:165–166. [Type species (monotypy) of *Ervilia* TURTON, 1822:56, pl. 19, fig. 4.]

DALL (1896), ROOIJ-SCHUILING (1972, 1973), and DAVIS (1973) present synonymies, a diagnosis, and distributional information for this species.

The type of *Mya nitens* was first described from specimens found in Dunbar, Scotland. FORBES & HANLEY (1853), however, believed such shells to have been brought to Europe in ballast sand from the Caribbean. This hypothesis was accepted by ROOIJ-SCHUILING (1973) and DAVIS (1973) as the only plausible explanation for the lack of new records for this species in the northeast Atlantic Ocean. *Ervilia castanea* is the only species of the genus that occurs in British waters (ROOIJ-SCHUILING, 1973; BABIO & BONNIN, 1987).

We have selected syntypes from the Royal Scottish Museum (RSM) that were previously in the collection of
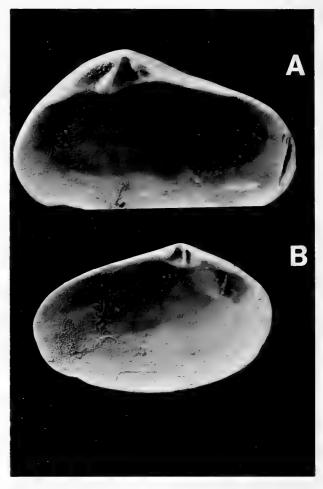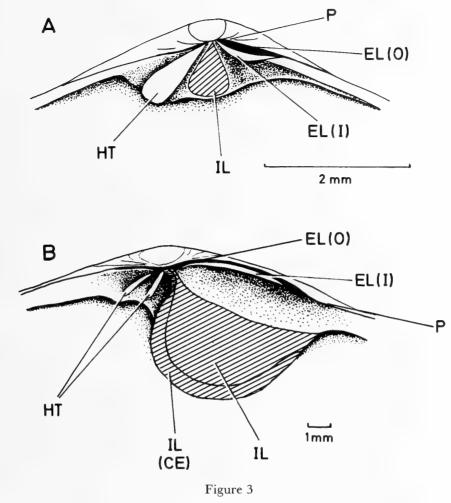
Figure 2

Ervilia castanea (Montagu, 1803). A. **Lectotype (herein)** of *Donax castanea* Montagu, 1803; internal of right valve, 10.4 mm length, 6.5 mm height; Devon, England; Royal Albert Memorial Museum, Exeter 3729. B. Paralectotype; internal of left valve, 8.8 mm length, 5.5 mm height; same locality and catalogue number as lectotype.

William Bean, a contemporary of Montagu (DEAN, 1936). We cannot prove this material was studied by Montagu, but owing to the very few specimens collected in the region and the association with Bean and Montagu, it does seem highly probable that this was the case. These RSM syntypes were reported by ROOIJ-SCHUILING (1972) as "possible paratypes." Syntypic specimens were not located in the British Museum (Natural History) (S. Morris, personal communication, January 1988) or the Royal Albert Memorial Museum, Exeter (J. D. Taylor, personal communication, July 1989).

Lectotype (herein): RSM 1866.21a.43; right valve; length = 7.0 mm, height = 4.4 mm (Figure 1A, B). Paralectotypes (additional specimens from lectotype lot, RSM 1866.21a.43); 1 intact pair and 2 left valves. Type locality:

Figure 3

Detail of hinge plates of the right valve. A. *Ervilia castanea* (Montagu, 1803) (after MORTON, in press). B. *Scrobicularia plana* (da Costa) (after TRUEMAN, 1953). Key: EL(I), inner element of external ligament; EL(O), outer element of external ligament; HT, hinge tooth; IL, inner ligament; IL(CE), cut edge of inner ligament; P, periostracum.

SCOTLAND, Lothian region, Dunbar; ca. 56°00′N, 02°30′W. The distribution of *Ervilia nitens* appears to encompass the western Atlantic Ocean and the Caribbean Sea (ROOIJ-SCHUILING, 1973; DAVIS, 1973).

Ervilia castanea (Montagu, 1803)

(Figures 2, 3A, 4)

Donax castanea MONTAGU, 1803:573, pl. 17, fig. 2.

Diagnoses and distributional information for *Ervilia castanea* are provided in TEBBLE (1966), ROOIJ-SCHUILING (1973), BABIO & BONNIN (1987), and MORTON (in press).
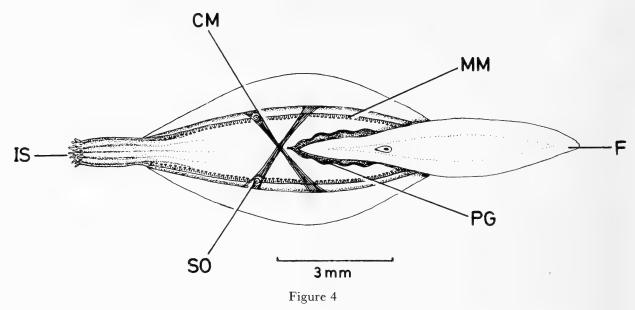
As with *Ervilia nitens,* and in spite of several taxonomic treatments of this species, a lectotype has never been selected. Syntypes from the Montagu collection were found in the Royal Albert Memorial Museum, Exeter (RAME) glued to their original card (catalogue No. 3729) (see DEAN, 1936).

Lectotype (herein): RAME 3729; right valve; length = 10.4 mm, height = 6.5 mm (Figure 2A). Paralectotype (attached to same card as lectotype); left valve; length = 8.8 mm, height = 5.5 mm (Figure 2B). Type locality: ENGLAND, Devon; ca. 50.2°N, 04.0°W.

Anatomical Features of *Ervilia castanea*

MORTON (in press) identified two important anatomical features that clearly separate *Ervilia* from the Mesodesmatidae, *i.e.,* the ligament and a cruciform muscle. Other details of the general morphology support this distinction.

The ligament and hinge plate: Hinge narrow to robust; left valve with two small anterior teeth separated by a deep socket (Figure 2B); right valve with large anterior tooth that interlocks into socket of left valve (Figures 2A, 3A); resilifer directly below beaks; small tubercle posterior of resilifer in both valves; obscure lateral teeth present in both valves.

Figure 4

Ervilia castanea (Montagu, 1803). Ventral view showing cruciform muscle. Key: CM, cruciform muscle; F, foot; IS, inhalant siphon; MM, mantle margin; PG, pedal gape; SO, sense organ (after MORTON, in press).

The ligament (Figure 3A) is complex and comprises a posteriorly directed (opisthodetic) external element (EL) and an amphidetic internal element (IL). The external element comprises an outer layer [EL(O)] and an inner layer [EL(I)] and is overlain by thin periostracum (P).

The cruciform muscle: Posteroventrally, in the region of the left and right mantle fusion between the inhalant siphon and pedal gape, the left and right shell valves are united by a cruciform muscle (Figure 4, CM). It comprises two compact bundles of muscles extending diagonally between the shell valves and crossing over at the midline of pallial fusion. Close to the shell, the posterior ends of the bundles each possess a sense organ (SO). The cruciform muscle of *Ervilia castanea* has been described by MORTON (in press) who also describes the sense organ and shows that it is "open" like that of *Scrobicularia,* as opposed to "closed" as is the case in *Donax, Tagelus,* and *Sanguinolaria* (FRENKIEL, 1979; FRENKIEL & MOUEZA, 1984).

Other features: The siphons are long and separate and formed by fusion of the inner mantle folds only (Type A) (YONGE, 1957, 1982). The ctenidia are large, homorhabdic, eulamellibranch, and non-plicate and the ciliary currents are of Type C(1) (ATKINS, 1937). The labial palps are small and the ctenidial-labial junction is of Category 3 (STASEK, 1963). The stomach is of Type V (PURCHON, 1987) but much simplified in this small species (MORTON, in press).

Alcohol preserved specimens of this species collected in the Azores are vouchered in the Santa Barbara Museum of Natural History (SBMNH 35147).

DISCUSSION

MONTAGU (1803) first described *Donax castanea* and later *Mya nitens* (MONTAGU, 1808). The latter is the type species (monotypy) of *Ervilia* Turton, 1822, which was placed in the Donacidae by FORBES & HANLEY (1853), and in the Paphiidae by SMITH (1885). DALL (1895) relocated *Ervilia* in the Mesodesmatidae and erected a new subfamily Erviliinae, which also included *Coecella* Gray, 1853, formerly placed in the Mactridae. LAMY (1914) agreed that both genera were members of the Mesodesmatidae but made no mention of the Erviliinae. Placement of *Ervilia* and *Coecella* in the Mesodesmatidae by both authors was on the basis of shell features, although DALL (1898) admitted the "nomenclature of the genera comprised in this family has always been more or less confused."

DALL (1911) erected the genus *Argyrodonax* in the Erviliinae based on a single specimen of *A. haycocki* from Bermuda. DALL (1924) also erected *Rochefortina* as a subgenus of *Rochefortia* (Montacutidae) but DALL *et al.* (1938) subsequently elevated *Rochefortina* to generic rank and placed it in the Erviliinae. IREDALE (1930) introduced the new genus *Spondervilia* without a description but named *Ervilia australis* Angas, 1877, as the type species. DALL *et al.* (1938) placed *Spondervilia* as a subgenus of *Ervilia* and differentiated the former by the presence of anterior radial sculpture. This assemblage of poorly known genera constitutes the Erviliinae (KEEN, 1969), a group with little taxonomic commendation. ROOIJ-SCHUILING (1972, 1973) ranked both *Spondervilia* and *Rochefortina* as junior subjective synonyms of *Ervilia,* leaving only *Argyrodonax, Coecella,* and *Ervilia* as members of the Erviliinae.

FRENKIEL (1979) has argued that the presence of a

cruciform muscle is diagnostic for the Tellinoidea. Researches on hitherto presumed tellinoideans without a cruciform muscle, *i.e.*, some members of the Solecurtidae Orbigny, 1846 (*e.g., Pharus* and *Sinonovacula* [FRENKIEL, 1979; MORTON, 1984]) have shown these to be solenoideans. The presence of a cruciform muscle in *Ervilia castanea,* therefore, firmly argues for relocation of the species into the Tellinoidea. Further, the cruciform muscle sense organ of the Donacidae is closed, but open in all others, arguing against placement in this family as proposed by MONTAGU (1803) and FORBES & HANLEY (1853). Representatives of the Tellinidae, Donacidae, and Psammobiidae possess an external ligament only. Representatives of the Scrobiculariidae and the Semelidae possess a ligament with both external and internal components.

TRUEMAN (1953) considered *Scrobicularia* to be a member of the Semelidae, a view with which BOSS (1972) concurred and which COAN (1988) formally proposed. The ligament of *Scrobicularia* (Figure 1B) is similar to that of *Ervilia,* although the arrangement of hinge teeth differs.

Like *Ervilia,* semelids are characterized by external and internal elements in the ligament and weakly developed hinge teeth (TRUEMAN, 1953; BOSS, 1972). The genus *Semele* is characterized by plicate ctenidia, whereas *Scrobicularia* has homorhabdic, non-plicate ctenidia (RICE, 1897; BOSS, 1972). Conversely, *Scrobicularia* is represented by deep-burrowing species with exceedingly long siphons used in deposit feeding from the sediment-water interface (YONGE, 1949). *Ervilia* is thus differentiable from both these genera and in the absence of detailed anatomical information (*e.g.,* cruciform muscle sense organ) concerning the other genera of the Semelidae (*i.e., Abra, Cumingia, Leptomya, Montrouzieria, Semelina,* and *Theora*), we propose that *Ervilia* be retained but relocated in the Semelidae.

ROOIJ-SCHUILING (1977) reported upon *Monterosatus* Beu, 1971, another genus of small mesodesmatids with an internal and external ligament. She notes that "... *Monterosatus* and *Ervilia* more or less resemble the Tellinidae in habits ...." When wet preserved specimens become available, thus allowing anatomical examination, especially in reference to the presence of a cruciform muscle, it is possible that *Monterosatus* will also be relocated in the Tellinoidea.

With removal of *Ervilia* from the Mesodesmatidae, we propose that the Erviliinae Dall, 1895, be abandoned and the remaining constituent genera, *Coecella* and *Argyrodonax,* be placed in the Mesodesmatinae. A thorough reassessment of the Mesodesmatoidea, as proposed by YONGE & ALLEN (1985), must now take place, since this paper casts serious doubt on the presently adopted classification of the group.

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First Occurrence of the Tethyan Bivalve

Nayadina (*Exputens*) in Mexico, and a

Review of All Species of This

North American Subgenus

by

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Abstract. The malleid bivalve *Nayadina* (*Exputens*) has Old World Tethyan affinities but is known only from Eocene deposits in North America. *Nayadina* (*Exputens*) is reported for the first time from Mexico. About 50 specimens of *N.* (*E.*) **batequensis** sp. nov. were found in warm-water nearshore deposits of the middle lower Eocene part of the Bateque Formation, just south of Laguna San Ignacio, on the Pacific coast of Baja California Sur.

The new species shows a wide range of morphologic variability especially where the beaks and auricles are located and how much they are developed. A review of the other species of *Exputens*, namely *Nayadina* (*E.*) *llajasensis* (Clark, 1934) from California and *N.* (*E.*) *ocalensis* (MacNeil, 1934) from Florida, Georgia, and North Carolina, revealed that they also have a wide range of morphologic variability. *Nayadina* (*E.*) *alexi* (Clark, 1934) is shown, herein, to be a junior synonym of *N.* (*E.*) *llajasensis*.

The presence of a byssal sinus is recognized for the first time in *Exputens*. An epifaunal nestling mode of life, with attachment by byssus to hard substrate, can now be assumed for *Exputens*.

INTRODUCTION

The macropaleontology of Eocene marine deposits in Baja California Sur, Mexico, is largely an untouched subject. Recent collecting by the author and Robert Demetrion from outcrops of the Eocene Bateque Formation in this area has resulted in the discovery of a varied and rich macrofauna. During field work, numerous specimens of the malleid bivalve *Nayadina* (*Exputens*) **batequensis** sp. nov. were found. *Exputens,* a warm-water bivalve with Old World Tethyan affinities (PALMER, 1967), is restricted to North America. Although two uncommon species had been reported from California, these two species are herein shown to be the same. *Exputens* is known also from one, uncommon species in the southeastern United States. Discovery of this interesting but scarce subgenus in Baja California Sur, therefore, represents a significant new find.

Attempts to identify the *Exputens* material of the Bateque Formation at the specific level were met with difficulty because of the incomplete knowledge of the existing species. It became necessary to thoroughly examine them, and after such a study, it was found that the Bateque material belongs to a new species.

The intent of this paper is not only to report the new stratigraphic and geologic occurrence of a new species of *Exputens* but also to revise the description of this subgenus, as well as the description of each of its other species. These revisions are based on new material, as well as a restudy of type material. Recognition of previously undetected morphologic features common to all these species also allows for new insights as to how *Exputens* lived. In addition, the wide range in morphologic variation in the other species is photographically documented.

Abbreviations used for catalog and locality numbers are as follows: CSUN, California State University, Northridge; IGM, Instituto de Geología, Universidad Autónoma Museum de México; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; UCLA, University of California, Los Angeles (collections
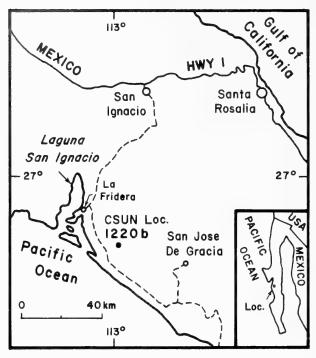
Figure 1

Index map to California State University, Northridge (CSUN) collecting locality 1220b, Bateque Formation, Baja California Sur, Mexico (after SQUIRES & DEMETRION, 1989).

now housed at the Natural History Museum of Los Angeles County); UCMP, University of California Museum of Paleontology, Berkeley; UCR, University of California, Riverside; UF, Florida Museum of Natural History, University of Florida, Gainesville; USNM, U.S. National Museum of Natural History, Smithsonian Institution.

MATERIALS

A total of 50 specimens of *Nayadina* (*Exputens*) *batequensis* were found in the Bateque Formation at locality CSUN 1220b, which is about 75 km southwest of San Ignacio, Baja California Sur, Mexico (Figure 1). Ten of these were too fragmental to be useful. Of the remaining specimens, there are about equal numbers of left and right valves. Two specimens are articulated.

A total of 35 specimens of *Nayadina* (*E.*) *llajasensis* (Clark, 1934) were studied. Five of the specimens are the primary type material from locality UCMP 7004, northern Simi Valley, southern California. The other specimens, except for one, are from this same locality and include 25 specimens borrowed from LACMIP and four more collected by the author. A single specimen was collected by the author from locality CSUN 473, also in northern Simi Valley. Four of the specimens were too fragmental to be useful. Of the remaining specimens, there are roughly equal numbers of left and right valves. Eight specimens are articulated.

Only four specimens of *Nayadina* (*E.*) *alexi* (Clark, 1934) were available for study, and they represent the primary type specimens from locality UCMP A-1007, central California. Three of the specimens are left valves and one is a right valve.

A total of 19 specimens of *Nayadina* (*E.*) *ocalensis* (MacNeil, 1934) were studied. Three of these are the primary type material from localities USGS 6812 and 12751, northern Florida, and the rest came from various localities examined by the University of Florida, Gainesville. Five of the specimens have well-indurated matrix covering the ligamental area. Of the remaining specimens, four are left valves and 10 are right valves.

DEPOSITIONAL ENVIRONMENT AND GEOLOGIC AGE OF THE BATEQUE SPECIMENS

The specimens of *Nayadina* (*E.*) **batequensis** in the Bateque Formation were found at locality CSUN 1220b, which is between 96 and 145 m above the base of the exposures of the formation in this area. The specimens were found in several lenses of fossiliferous, very fine-grained sandstone surrounded by bioturbated, very fine-grained sandstone. Associated macrofauna included stromatolites, coralline algae, calcareous sponges, colonial and solitary scleractians, encrusting and branching bryozoans, thick-shelled gastropods and bivalves, nautiloids, crabs, spatangoids, and sea urchin spines. A new species of calcareous sponge (SQUIRES & DEMETRION, 1989), new species of gastropods (SQUIRES & DEMETRION, 1990), and new taxa of bivalves (SQUIRES & DEMETRION, in press; SQUIRES, in press) have been described from this locality. The fossiliferous lenses represent storm-deposit concentrations in an inner shelf warm-water environment, and the amount of post-mortem transport was not great (SQUIRES & DEMETRION, in press). Lack of transport is also supported by the presence of articulated specimens of *N.* (*E.*) **batequensis**, as well as by the approximately equal number of unabraded left and right valves of this bivalve.

The fossiliferous lenses at locality 1220b contain planktonic foraminifera indicative of the early Eocene *Globorotalia aragonensis* or *G. pentacamerata* Zone of STAINFORTH *et al.* (1975), which is equivalent to the P8 or P9 Zone as used by BERGGREN *et al.* (1985) (SQUIRES & DEMETRION, 1990).

MODE OF LIFE OF *Exputens*

Of the previous workers, only CLARK (1934:271) offered an opinion as to how *Exputens* lived. He concluded that it was probably a nestler, based on surface irregularities in the shell, variability in form, generally elongate shape, and the lack of any well-defined byssal sinus. Presumably, he considered *Exputens* to be an unattached nestler.

In the present study, however, a byssal sinus is recognized for the first time in *Exputens*. Furthermore, it is present in all the species of this subgenus, which may have

been byssate epifaunal nestlers or, possibly, byssate fissure dwellers. Such bivalves commonly inhabit nearshore, shallow-water environments where firm substrate is available, as in reefs or on the roots of marine plants (KAUFFMAN, 1969).

Abundant fragments of reef corals are associated with *Nayadina (E.)* **batequensis** in the Bateque Formation. In addition, there is a strong possibility that marine plants were associated as well, because *Pycnodonte* oysters with possible scars of marine plants were found with *Exputens* at locality CSUN 1220b (SQUIRES & DEMETRION, in press). All valves of *N. (E.)* **batequensis** have a distinct groove that shows the former position of the byssal sinus. The distinctness of the groove indicates that the byssus was robust. In the relatively high-energy nearshore environment in which this species lived, a robust byssus would have been necessary to provide adequate attachment.

Abundant shell debris could have served as firm substrate for the numerous specimens of *Nayadina (E.)* *llajasensis* from the "Stewart bed" at locality UCMP 7004 in the Llajas Formation. SQUIRES (1981, 1984) reported that the macrofossils in the "Stewart bed" at this locality (=locality CSUN 374) represent a shelf-slope break paleocommunity consisting of at least 50 species of mollusks. Many bivalves, including *Exputens,* are articulated and large. They were able to grow to maturity in this moderately calm-water environment. Many valves of *N. (E.)* *llajasensis* have only a weakly developed groove that shows the former position of the byssal sinus. The weak development of the groove indicates that the byssus was not very robust. In the moderately calm-water environment in which this species lived, a moderately robust byssus would have provided adequate attachment for most of the specimens.

No detailed information is available concerning the paleoenvironment of *Nayadina (E.) ocalensis.* However, it is likely that *N. (E.) ocalensis* lived in a relatively high-energy environment much like that of *N. (E.)* **batequensis** because the groove that shows the former position of the byssal sinus is distinct in both. The presence of small pebbles of calcareous material and foraminiferal coquina matrix that fills the interior of some of the valves of *N. (E.) ocalensis* also supports a relatively high-energy environment interpretation.

Some modern malleids are byssate and epifaunally attached to other shells or coralline rock (BOSS & MOORE, 1967; YONGE, 1968; KEEN, 1971). Two of the most commonly occurring examples are *Malleus (Malleus) malleus* (Linné) and *M. (Malvufundus) regula* (Forskål). Both are widely distributed in the tropical Indo-Pacific area. The shells of these species are vertically disposed, rest on the umbonal-byssal surface (*i.e.,* dorsal surface), and are firmly attached to rocky surfaces (YONGE, 1968). Their shells in the ligamental area are somewhat similar to those of *Exputens,* although they have a byssal sinus that is much stronger than in *Exputens* and deep and long enough to qualify as a notch.

Figure 2

Reconstruction of the living position of *Nayadina (Exputens).* Right-valve exterior view, ×2.1, shows the dorsal side of shell attached by a byssus to a shell fragment (*i.e.,* hard substrate). Diagram is based on paratype, IGM 5114 of *N. (E.)* **batequensis** sp. nov., shown in Figures 14–16.

Based on morphologic similarities between *Exputens* and modern byssate malleids, as well as on available paleoecologic data concerning *Exputens,* a reconstruction of the living position of *Nayadina (Exputens)* is given in Figure 2. Having *Exputens* rest on its dorsal surface is also in keeping with the fact that articulated and even some single-valve specimens of *Exputens* are stable in that position.

SYSTEMATIC PALEONTOLOGY

Family MALLEIDAE Lamarck, 1819

Genus *Nayadina* Munier-Chalmas, 1864

Type species: By monotypy, *Nayadina herberti* Munier-Chalmas, 1864.

Subgenus *Exputens* Clark, 1934

Type species: By subsequent designation (VOKES, 1939), *Exputens llajasensis* Clark, 1934.

Description: Small to large size, subquadrate elongate to triangular shape, equivalved, inequilateral. Anterior end usually elongated, and posterior dorsal margin usually raised and laterally inflated. Both ends of shell elongated with anterior end laterally inflated or not, or only posterior end elongated with anterior end laterally inflated. In a few specimens, both ends of shell elongated and both posterior and anterior dorsal margins raised and inflated, causing dorsal margin of shell to appear depressed in ligamental area. Valves smooth or with irregular commarginal lamellae. Beaks prosogyrate, very low to very inflated, usually in posterior half of shell but ranging from extreme posterior end to slightly anterior of center. Single auricle on each valve very low to very projecting, usually in posterior half of valve but ranging from very near posterior end to slightly anterior of center. Auricles offset from and usually posterior to beaks, just anterior to the beaks, directly above them, or even covering them. Auricles connected to beak area by one curved or fairly straight ridge.

Ligamental area projected along hinge line, forming an overhanging platform. Posterior part of ligamental area flat to concave to ridgelike, triangular, and projected dorsally owing to coincidence with auricle. Ligamental pit intrusive, concave, deep to moderately deep, with apex near beak. Ligamental pit mostly or, in rare cases, entirely anterior to beak. Length of ligamental pit (measured parallel to hinge line) approximately one-eighth to one-fourth of valve length. Margins of ligamental pit straight or undulatory. Anterior margin of ligamental pit commonly strongly raised with one dorsally directed toothlike projection on hinge line. Byssal groove equally developed on each valve, just anterior to raised anterior margin of ligamental pit and extending from beak to hinge line. Byssal groove narrow, shallow, distinct to fairly distinct, becoming more pronounced ventrally where it ends in small, shallow byssal sinus. In some specimens, anterior ventral corner of byssal groove ventrally directed with one toothlike projection on hinge line. Dorsal margin of shell immediately anterior to byssal sinus usually inflated and, in some cases, very strongly inflated. Monomyarian. Muscle scar subcircular to elongate, near ventral margin and below ligamental area, but posterior to byssal sinus. Rarely, one pallial rib in region posterior from ligamental pit area to dorsoposterior corner of muscle scar. Prismatic outer shell underlaid by nacreous lamellar layer. Shell length up to 53.8 mm, shell height up to 29 mm.

Discussion: A revised description of *Exputens* is given above because of new findings made during the present study. The most important of these findings is the presence of a byssal sinus, which is best developed in *Nayadina (E.) batequensis* and *N. (E.) ocalensis*. As the shell grew, the byssal sinus in each valve was continually infilled with shell material and became a groove. The sinus itself is a small indentation of the hinge line and is only observable in a dorsal view of the hinge line.

Some modern-day members of the family Malleidae, such as *Malleus (M.) malleus* and *M. (Malvufundus) regula,* have a byssal notch located anterior to the ligamental area and anterior to the adductor muscle scar. By analogy, it is interpreted that these same relationships hold for *Exputens.* Such observations now allow for an understanding of the proper orientation of the valves of *Exputens.* As noted by MacNeil (1934) and Nicol & Shaak (1973), there has been much confusion in the literature regarding which is the anterior end and which is the posterior end of the shell of *Exputens.* Most authors have mainly relied on the assumption that the beaks and auricles are in the anterior part of the shell. With few exceptions, however, just the reverse is true: usually the beaks and auricles are located in the posterior part of the shell.

Prosogyrate beaks and an outer prismatic shell layer in *Exputens* are recognized for the first time in this report.

Clark (1934) and Hertlein & Cox (1969) reported that *Exputens* is dimyarian. In this study, however, no

specimens of *Exputens* were observed to have more than a single muscle scar.

The relationship between ligamental pit length and valve length in *Exputens* is different for each species. Within each species, the relationship is fairly uniform, regardless of specimen size.

There is a wide range of variability in *Exputens* in terms of where the beaks and auricles are located and how inflated and projecting they are. There is also much variability as to which part of the shell is elongate, raised, or inflated.

Previously, Hertlein & Cox (1969) reported *Exputens* only from the middle Eocene of California and Jamaica. Unfortunately, they did not cite the source for the Jamaican occurrence, and it could not be found during the course of this study.

Material: *Exputens* includes *Nayadina (E.) llajasensis* (Clark) [which includes *N. (E.) alexi* (Clark)], *N. (E.) ocalensis* (MacNeil), and *N. (E.) batequensis*.

Distribution: Middle lower Eocene ("Capay Stage," equivalent to Ypresian Stage) to lower middle Eocene ("Domengine Stage," equivalent to lower Lutetian Stage) on the west coast of North America; upper Eocene (Jackson Stage, equivalent to upper Bartonian to Priabonian Stages) in the southeastern United States.

Nayadina (Exputens) **batequensis** Squires, sp. nov.

(Figures 3–25)

Diagnosis: Small size, triangular to elliptical shape, spirally curved short auricles usually near posterior end of shell, beaks and auricles anterior of center of shell in some specimens, margins of ligamental pit straight, and in both valves a distinct groove showing former positions of byssal sinus.

Description: Mostly small size, triangular to elliptical shape, less commonly subquadrate elongate shape, equivalved, inequilateral. Anterior end usually elongated, and posterior dorsal margin usually raised and inflated. Both ends of shell elongated with anterior end laterally inflated or not, or only posterior end elongated. Rarely, both ends of shell elongated and both posterior and anterior dorsal margins raised, causing dorsal margin of shell to appear depressed in ligamental area. Valves nearly smooth with closely spaced growth lines or rough owing to low commarginal lamellae accentuated by weathering. Beaks prosogyrate, fairly prominent, usually in posterior half of shell, but range from extreme posterior end to slightly anterior of center. Short auricle on each valve usually small but moderately prominent to very projecting, usually in posterior half of valve but ranging from near the posterior end to slightly anterior of center. Auricles offset from and usually posterior to beaks, but occasionally just anterior to beaks or directly above them. In most specimens, auricles

connected to beak area by prominent spiral ridge along anterior margin of ligamental pit.

Ligamental area projected along hinge line, forming overhanging platform. Posterior part of ligamental area flat or ridgelike, triangular, and projected dorsally owing to coincidence with auricle. Ligamental pit intrusive, concave, usually very prominent, and mostly or, in rare cases, entirely anterior to beak. Length of ligamental pit slightly less than approximately one-fourth of valve length. Margins of ligamental pit straight. Byssal groove equally developed on each valve, just anterior to raised anterior margin of ligamental pit and extending to beak. Byssal groove narrow, shallow, distinct, becoming more pronounced ventrally where it ends in small, shallow sinus. In some specimens, anterior ventral corner of byssal groove ventrally directed with one toothlike projection on hinge line. Dorsal margin of shell immediately anterior to byssal sinus usually strongly inflated. Rarely, one pallial rib in region posterior from ligamental pit area to dorsoposterior corner of muscle scar. Muscle scar subcircular to elongate, near ventral margin, below ligamental area, and posterior to byssal sinus. Shell length up to 36 mm (most not over 20 mm), shell height up to 23 mm (most not over 12 mm).

Discussion: Seven variants were found. The triangular form of the holotype (Figures 3–5) is the most common variant. This variant is also shown in Figures 6–8. The other variants, with the beak area becoming progressively more anteriorly located, are shown in Figures 14–25. Most of these variants, except for the one shown in Figure 13, are confined to either single specimens or only a few specimens. The most unusual variant, shown in Figures 20–25, has the beak anterior to the center of the shell and can have a very projected auricle.

Nayadina (*E.*) **batequensis** differs from *N.* (*E.*) *llajasensis* in its smaller size, forms with a triangular shape, smaller and more spirally curved auricles, posterior part of ligamental area that can be ridgelike, beaks and auricles that can be slightly anterior of the center of the shell, auricles that are never covered by the beaks, and in both valves a more common occurrence of a distinct groove that shows the former position of the byssal sinus.

Nayadina (*E.*) **batequensis** differs from *N.* (*E.*) *ocalensis* in having smaller size, forms with a triangular shape, auricles that can be anterior to the beaks, auricles less rectangularly shaped, auricles that can be more projecting, dorsal margin of shell immediately anterior to byssal sinus more strongly inflated, length of ligamental pit slightly less than approximately one-fourth rather than one-eighth of valve length, and straight margins along the ligamental pit.

Holotype: IGM 5108 = plastoholotype, LACMIP 8294.

Type locality: Locality CSUN 1220b, just south of Laguna San Ignacio, Baja California Sur, Mexico.

Paratypes: IGM 5109–5119 = plastoparatypes, LACMIP 8295–8305.

Distribution: West Coast "Capay Stage," equivalent to middle lower Eocene (Ypresian Stage): Bateque Formation, Baja California Sur, Mexico, locality CSUN 1220b.

Nayadina (*Exputens*) *llajasensis* (Clark, 1934)

(Figures 26–46)

Exputens llajasensis CLARK, 1934:270–271, pl. 37, figs. 11–18; VOKES, 1939:51.
Exputens alexi CLARK, 1934:271–272, pl. 37, figs. 19–24; VOKES, 1939:51, pl. 2, figs. 2, 5, 9.
Nayadina (*Exputens*) *llajasensis* (Clark): HERTLEIN & COX, 1969:331, fig. C55-7; GIVENS, 1974:44, pl. 1, fig. 9; MOORE, 1983:A86–A87, pl. 26, figs. 10, 13; SQUIRES, 1984:43, figs. 10h–i.
Nayadina (*Exputens*) *alexi* (Clark): MOORE, 1983:A86, pl. 26, figs. 8–9.
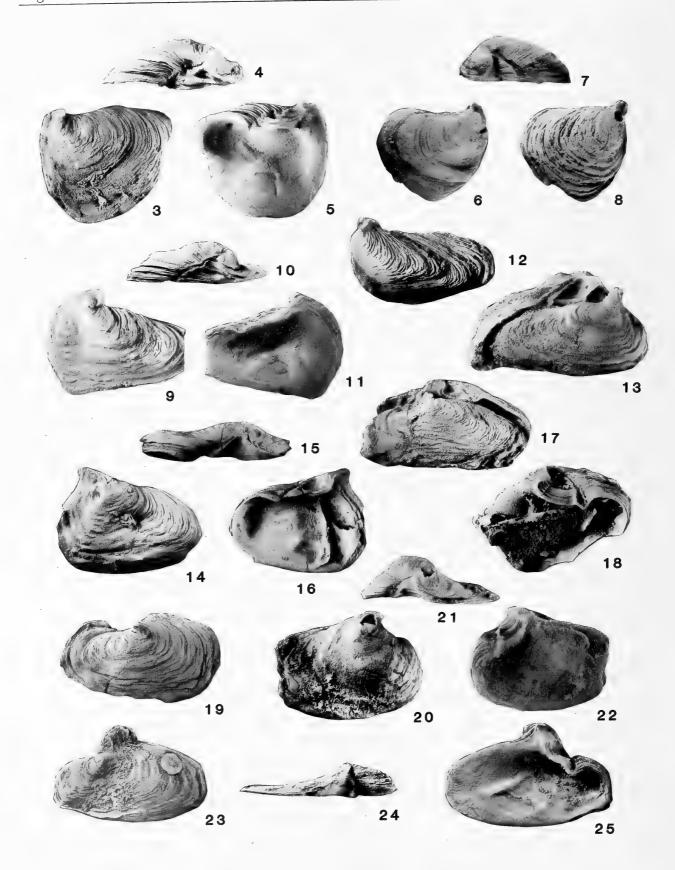
Supplementary description: Mostly large size, subquadrate elongate shape, equivalved, inequilateral. Anterior end usually elongated, and posterior dorsal margin usually raised and laterally inflated. Both ends of shell elongated with anterior end laterally inflated or not, or only posterior end elongated with anterior end laterally inflated. Occasionally, both ends of shell elongated and both posterior and anterior dorsal margins raised and inflated, causing dorsal margin of shell to appear depressed in ligamental area. Valves with closely spaced growth lines and rough with irregular commarginal lamellae, especially in posterior part of shell. Beaks prosogyrate, very low to very inflated, usually in posterior half of shell but ranging from extreme posterior end to center. Single auricle on each valve bladelike, low to prominent, usually in posterior half of valve or at the center. Auricles usually offset and posterior to beaks. In some specimens, exterior of auricles partially or completely covered by beaks. Auricles usually connected to beak by straight or curving ridge.

Ligamental area projected along hinge line, forming overhanging platform. Posterior part of ligamental area flat or rarely concave and projected dorsally owing to coincidence with auricle. Ligamental pit intrusive, concave, usually very deep, and mostly anterior to beak. Length of ligamental pit approximately one-fourth of valve length. Margins of ligamental pit straight. Byssal groove developed equally on each valve, just anterior to raised anterior margin of ligamental pit and extending to beak. Byssal groove narrow, shallow, and usually weakly developed, becoming more pronounced ventrally where it ends in broad, shallow sinus. In some specimens, anterior ventral corner of byssal groove ventrally directed with one toothlike projection on hinge line. Dorsal margin of shell immediately anterior to byssal sinus usually inflated. Muscle scar elongate, large, near ventral margin, below ligamental area, and slightly posterior to byssal sinus. Prismatic outer shell

layer underlaid by nacreous lamellar layer. Shell length up to 53.8 mm (many about 50 mm), shell height up to 29 mm.

Discussion: Five variants of this species were found. The form of the holotype is the most common variant (Figures 26–30, 38–46). The other variants are mainly confined to single specimens, shown in Figures 31–36, with the beak area becoming progressively more anteriorly located. In the most unusual variant the anterior and posterior ends are equally elongate, only the anterior end is laterally inflated, and the projecting beaks engulf the auricles (Figures 35, 36).

CLARK (1934) also commented on the variability of this species and recognized three variants (A–C). CLARK's (1934) variant A is the form of the holotype. In this present report, Clark's variant B is included with the form of the holotype, but his variant C is regarded as distinct (Figure 33). CLARK (1934) reported that variant C is opisthogyrate, but actually it is prosogyrate.

The muscle scar of this species, previously unknown, is illustrated for the first time in Figure 29.

The four primary type specimens of *Nayadina (E.) alexi* show only a small amount of variation in morphology. All have the form of the holotype of *N. (E.) llajasensis* and are determined, for the first time, to be conspecific with *N. (E.) llajasensis*. The holotype of *N. (E.) alexi*, shown in Figures 38–40, is very similar to a specimen of *N. (E.) llajasensis* (Figure 41). A paratype of *N. (E.) alexi* (Figure 42) is essentially identical to a specimen of *N. (E.) llaja-sensis* (Figure 43), and another paratype of *N. (E.) alexi* (Figures 44, 45) is very similar to a specimen of *N. (E.) llajasensis* (Figure 46).

CLARK (1934) reported that *Nayadina (E.) alexi* could be distinguished from *N. (E.) llajasensis* on the basis of the following: the auricles are above the beaks in *N. (E.) alexi* but are offset from the beaks in *N. (E.) llajasensis,* the ligamental pit in *N. (E.) alexi* is less concave, and *N. (E.) alexi* is smaller. Actually, the auricles are offset from the beaks in *N. (E.) alexi,* and the amount of offset is similar to that in the holotype of *N. (E.) llajasensis*. The difference in concavity of the ligamental pit is just the result of spec-

imen size. The average shell height of *N. (E.) alexi* is 12 mm whereas in *N. (E.) llajasensis* it is 24 mm. The amount of ligamental pit concavity in the holotype of *N. (E.) alexi* (Figure 40) is 2.7 mm (measured vertically from the apex of the auricle to the ventral surface of the ligamental pit). The amount of ligamental pit concavity in an average specimen of *N. (E.) llajasensis* (Figure 28) is 5.5 mm. This paratype of *N. (E.) llajasensis* is twice the size of the holotype of *N. (E.) alexi* and, hence, has twice the amount of concavity in the ligamental pit.

The primary type specimens of *Nayadina (E.) alexi* represent juvenile forms whereas those of *N. (E.) llajasensis* are fully mature specimens. When specimen age is taken into consideration, any distinction between *N. (E.) alexi* and *N. (E.) llajasensis* is removed.

Nayadina (E.) llajasensis differs from *N. (E.)* **batequensis** in having larger size, no triangular forms, more blade-like auricles, larger and straighter auricles, beaks and auricles that are never anterior of center of the shell, beaks that can cover the auricles, posterior parts of ligamental area not ridgelike, and in both valves usually a less distinct groove that shows the former position of the byssal sinus.

Nayadina (E.) llajasensis differs from *N. (E.) ocalensis* in having beaks and auricles never anterior of center of the shell, beaks that can cover the auricles, length of ligamental pit approximately one-fourth rather than one-eighth of valve length, straight margins along the ligamental pit, posterior parts of ligamental area not ridgelike, and in both valves usually a less distinct groove that shows the former position of the byssal sinus.

Holotype: UCMP 32391. [Note: Holotype of *N. (E.) alexi* is UCMP 32386.]

Type locality: *Nayadina (E.) llajasensis*: Locality UCMP 7004, Las Llajas Canyon, just north of Simi Valley, Ventura County, southern California. [Note *Nayadina (E.) alexi*: Locality UCMP A-1007, Los Gatos Creek, Fresno County, central California.]

Paratypes: *Nayadina (E.) llajasensis*: UCMP 32389–32390, 32392–32393. *Nayadina (E.) alexi*: UCMP 32384–32385, 32387.

←

Explanation of Figures 3 to 25

Figures 3–25. *Nayadina (Exputens) batequensis,* CSUN locality 1220b. Figures 3–5: holotype, IGM 5108, right valve, ×2.3; Figure 3, exterior; Figure 4, dorsum; Figure 5, interior. Figures 6–7: paratype, IGM 5109, left valve, ×2.2; Figure 6, exterior; Figure 7, dorsum. Figure 8: paratype, IGM 5110, left valve exterior, ×3.5. Figures 9–11: paratype, IGM 5111, right valve, ×2; Figure 9, exterior; Figure 10, dorsum; Figure 11, interior. Figure 12: paratype, IGM 5112, right valve exterior, ×2.5. Figure 13: paratype, IGM 5113, left valve exterior, ×2.4. Figures 14–16: paratype, IGM 5114, right valve; Figure 14, exterior, ×2.1; Figure 15, dorsum, ×2.2; Figure 16, interior, ×2.1. Figure 17: paratype, IGM 5115, right valve exterior, ×1.8. Figure 18: paratype, IGM 5116, partial left valve interior, ×1.6. Figure 19: paratype, IGM 5117, left valve exterior, ×2.2. Figures 20–22: paratype, IGM 5118, right valve, ×1.9; Figure 20, exterior; Figure 21, dorsum; Figure 22, interior. Figures 23–25: paratype, IGM 5119, left valve; Figure 23, exterior, ×1.1; Figure 24, dorsum, ×1.2; Figure 25, interior, ×1.2.

Distribution: West Coast "Capay Stage" and "Domengine Stage," equivalent to middle lower to lower middle Eocene (Ypresian to lower Lutetian Stages). "Capay Stage": Juncal Formation, *Turritella uvasana infera* fauna, Pine Mountain area, Ventura County, southern California, locality UCR 4659 (GIVENS, 1974). "Domengine Stage": "Stewart bed," middle Llajas Formation shallow-marine (transgressive) facies, Simi Valley, Ventura County, southern California, at and in the vicinity of locality UCMP 7004 [=locality UCLA 2312 = locality CSUN 374], as well as at and in the vicinity of locality CSUN 473 (CLARK, 1934; SQUIRES, 1984); Domengine Formation, Fresno County, central California, locality UCMP A-1007 (CLARK, 1934).

Nayadina (*Exputens*) *ocalensis* (MacNeil, 1934)
(Figures 47–60)

Vulsella ocalensis MACNEIL, 1934:43, figs. 5–11; HARRIS, 1951:14, pl. 6, figs. 7, 7'.
Exputens ocalensis (MacNeil): NICOL & SHAAK, 1973:72–73, figs. 1–3; TOULMIN, 1977:316–317, pl. 56, fig. 6; PALMER & BRANN, 1965:143 (lectotype designated).

Supplementary description: Mostly medium size, subquadrate elongate shape, inequilateral. Anterior end usually elongated, and posterior dorsal margin usually raised and inflated. Both ends of shell elongated with anterior end laterally inflated or not, or only posterior end elongated. In one specimen, only the anterior dorsal area inflated. Valves smooth or with irregular commarginal lamellae. Beaks prosogyrate, low to moderately prominent and usually in posterior half of shell but ranging from near posterior end to, in rare cases, anterior part. Single auricle on each valve usually bladelike, usually with right-angle bend at dorsal posterior corner, low to moderately strongly projecting, usually in posterior half of valve or slightly anterior to center. Auricles offset and posterior to beaks, rarely directly above beaks. Auricles connected to beak by straight to curving ridge.

Ligamental area projected along hinge line, forming overhanging platform. Posterior part of ligamental area flattish to ridgelike and projected dorsally owing to coincidence with auricle. Ligamental pit intrusive, concave, very prominent, and mostly anterior to beak. Length of ligamental pit approximately one-eighth of valve length. Margins of ligamental pit commonly markedly undulatory. Anterior margin of ligamental pit commonly strongly raised with one dorsally directed toothlike projection on hinge line. Byssal groove equally developed in each valve, just anterior to raised anterior margin of ligamental pit and extending to beak. Byssal groove narrow, usually distinct, becoming more prominent ventrally where it ends in small, shallow byssal sinus. In some specimens, anterior ventral corner of byssal groove ventrally directed with one toothlike projection on hinge line. Dorsal margin of shell immediately anterior to byssal sinus usually moderately inflated. Muscle scar subcircular to elongate, along ventral margin, below ligamental area, and slightly posterior of byssal sinus. Shell length up to 47.6 mm, shell height up to 24 mm.
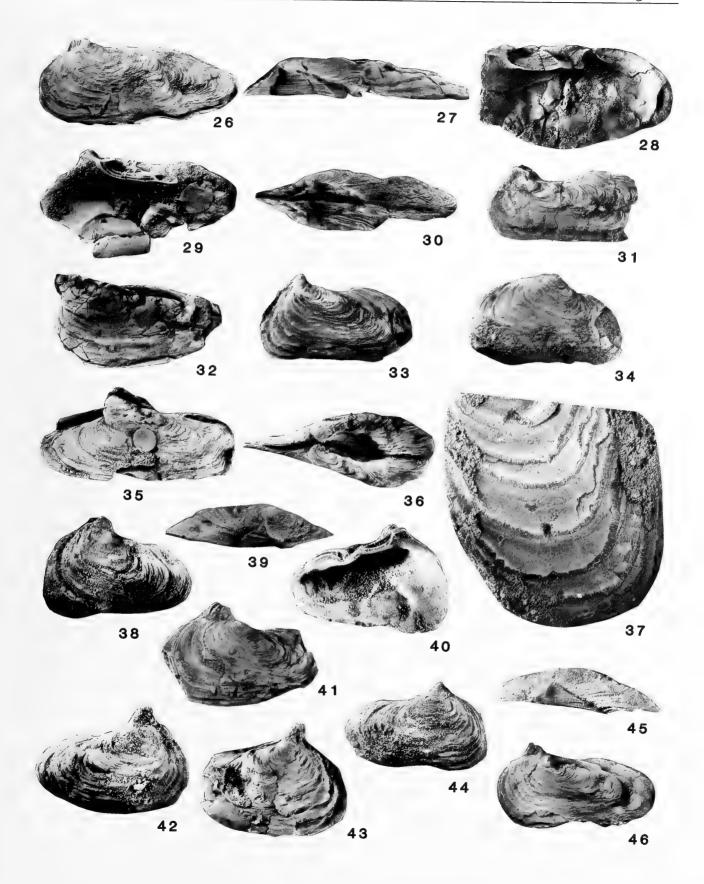
Discussion: Four variants of this species were found. The form of the lectotype is the most common variant (Figures 47–50). This form is also shown in Figure 51. The other variants are mainly confined to single specimens and are shown in Figures 52–60. The most unusual variant, shown in Figures 58–60, has the beak and auricle in the anterior part of the shell, and has an inflated anterodorsal part of the valve.
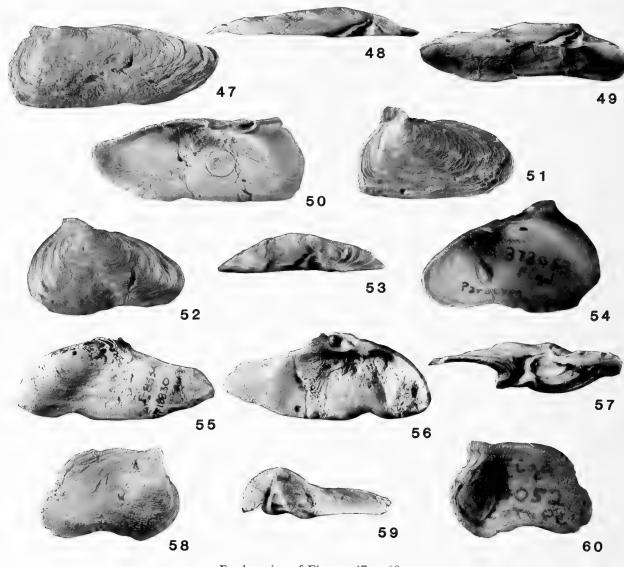
MACNEIL (1934) reported that the muscle scar of this species is anterior to the beak. Actually, it is posterior to the beak.

Nayadina (*E.*) *ocalensis* differs from *N.* (*E.*) **batequensis** in having no triangular forms, auricles never anterior to the beaks, auricles commonly more rectangular shaped, dorsal margin of shell immediately anterior to byssal sinus less strongly inflated, length of ligamental pit approximately one-eighth rather than slightly less than one-fourth

→

Explanation of Figures 26 to 46

Figures 26–46. *Nayadina* (*Exputens*) *llajasensis* (Clark, 1934), locality UCMP 7004, unless otherwise noted. Figure 26: holotype, UCMP 32391, right valve exterior, ×1. Figures 27–28: paratype, UCMP 32389, left valve; Figure 27, dorsum, ×1.5; Figure 28, interior, ×1.3. Figure 29: hypotype and topotype, LACMIP 8306, left valve interior, ×1.3. Figure 30: holotype, UCMP 32391, complete specimen, dorsum, ×1. Figure 31: hypotype and topotype, LACMIP 8307, right valve exterior, ×1.2. Figure 32: paratype, UCMP 32392, right valve exterior, ×1.2. Figure 33: paratype, UCMP 32390, right valve exterior, ×1. Figure 34: hypotype and topotype, LACMIP 8308, right valve exterior, ×1. Figures 35–36: hypotype and topotype, LACMIP 8309, ×1; Figure 35, right valve exterior; Figure 36, complete specimen, dorsum. Figure 37: hypotype and topotype, LACMIP 8310, partial right valve exterior showing outer prismatic layer, ×3. Figures 38–40: holotype, UCMP 32386 of *N.* (*E.*) *alexi* (Clark, 1934), locality UCMP A-1007, right valve; Figure 38, exterior, ×2; Figure 39, dorsum, ×2.4; Figure 40, interior, ×2.2. Figure 41: hypotype and topotype, LACMIP 8311, right valve exterior, ×1. Figure 42: paratype, UCMP 32384 of *N.* (*E.*) *alexi* (Clark, 1934), locality UCMP A-1007, left valve exterior, ×2.4. Figure 43: hypotype, LACMIP 8312, locality CSUN 473, left valve exterior, ×2.4. Figures 44–45: paratype, UCMP 32385 of *N.* (*E.*) *alexi* (Clark, 1934), locality UCMP A-1007, left valve; Figure 44, exterior, ×1.9; Figure 45, dorsum, ×2.2. Figure 46: paratype, UCMP 32393, right valve exterior, ×0.8.

Explanation of Figures 47 to 60

Figures 47–60. *Nayadina* (*Exputens*) *ocalensis* (MacNeil, 1934). Figures 47–50: lectotype, USNM 373052, locality USGS 12751, right valve; Figure 47, exterior, ×1.1; Figure 48, dorsum, ×1.2; Figure 49, oblique view of dorsum, ×1.2; Figure 50, interior, ×1.2. Figure 51: hypotype, UF 3481, quarry west of U.S. 441 at south edge of Kendrick, Marion County, Florida, right valve exterior, ×1.5. Figures 52–54: paratype, USNM 373053, locality USGS 6812, right valve; Figure 52, exterior, ×1.5; Figure 53, dorsum, ×1.6; Figure 54, interior, ×1.7. Figures 55–56: hypotype, UF 18830, Bell 1 quarry, Gilchrist County, Florida, left valve; Figure 55, exterior, ×1.1; Figure 56, interior, ×1.2. Figure 57: hypotype, UF 5709, Dickerson Limerock Mines, Alachua County, Florida, right valve dorsum, ×2.5. Figures 58–60: paratype, USNM 373052, locality USGS 12751, right valve; Figure 58, exterior, ×3; Figure 59, dorsum, ×3.2; Figure 60, interior, ×3.1.

of valve length, and undulatory margins along the ligamental pit.

Nayadina (*E.*) *ocalensis* differs from *N.* (*E.*) *llajasensis* in having beaks and auricles that can be anterior of center, auricles that are never covered by the beaks, posterior part of ligamental area that can be ridgelike, length of ligamental pit approximately one-eighth rather than one-fourth of valve length, undulatory margins along the ligamental pit, and in both valves a more common occurrence of a distinct groove that shows the former position of the byssal sinus.

Lectotype: USNM 373052, figs. 10–11 of MacNEIL (1934); designated by PALMER & BRANN (1965:143).

Type locality: Locality USGS 12751, Sumter Rock Co. quarry, just northeast of Sumterville, Sumter County, northern Florida.

Paratypes: USNM 373052 (=figs. 5–6 of MacNeil [1934]) and USNM 373053.

Distribution: Southeastern United States Jackson Stage, equivalent to upper Eocene (upper Bartonian and Priabonian Stages). Jackson Stage: Crystal River Formation (=Ocala Limestone, restricted, according to Puri [1957]), northern Florida, localities USGS 6812 and 12751 (MacNeil, 1934), Kendrick quarry (Nicol & Shaak, 1973), unspecified localities in Columbia, Suwannee, Dixie, Gilchrist, Alachua, Levy, Marion, Citrus, and Sumter Counties, northern Florida (Nicol & Shaak, 1973), and the following new localities: Newberry Corp. Pit 1, Dickerson Limerock Mines, Buda 1 Quarry, all from Alachua County, Florida, and Bell 1 Quarry, Gilchrist quarry, Florida; Toulmin collection locality Fla-1 (Toulmin, 1977); Ocala Limestone, southwestern Georgia (Nicol & Shaak, 1973); Castle Hayne Marl, unspecified localities in Pender and Wayne Counties, southeastern and north-central North Carolina (Nicol & Shaak, 1973).

ACKNOWLEDGMENTS

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APPENDIX

Localities Cited

CSUN 473: At elevation of 503 m (1650 ft) on a ridge, 320 m (1050 ft) north and 701 m (2300 ft) west of southeast corner of section 30, T3N, R17W, Santa Susana 7.5-minute quadrangle, 1969, northern Simi Valley, Ventura County, California. Locality is in the "Stewart bed" (SQUIRES, 1984:61). Llajas Formation. Age: Early middle Eocene ("Domengine Stage"). Collector: R. L. Squires.

CSUN 1220b: North side of a minor canyon, at an elevation of 120 m, on the west side of Mesa La Salina, 100 m above the bottom of the exposures of the Bateque Formation, approximately 1.25 km southeast of the intersection of 113°00′W and 26°45′N, San Jose de Gracia, Baja California Sur, Mexico, 1:50,000 quadrangle map (number G12A64), issued in 1983 under the authority of the Direccion General de Geografia. Bateque Formation. Age: Middle early Eocene ("Capay Stage"). Collectors: R. L. Squires and Robert Demetrion.

UCMP A-1007: Coarse sandstone reef, underlying and overlying shale, outcropping about 100 m from the mouth of a small gulley on the north bank of Los Gatos Creek, which is a few kilometers north of the town of Coalinga and in the NE ¼, sec. 10, T20S, R14E (CLARK, 1934: 272), Alcalde Hills 7.5-minute quadrangle, 1969, Fresno County, central California. Domengine Formation. Age: Early middle Eocene ("Domengine Stage"). Collector: Alex Clark.

UCMP 7004: At elevation of 518 m (1700 ft) on a small cliff on south side of a side canyon to Las Llajas Canyon, 594 m (1950 ft) north and 556 m (1825 ft) east of southeast corner of section 29, T3N, R17W, Santa Susana 7.5-minute quadrangle, 1969, northern Simi Valley, Ventura County, southern California. Locality is in the "Stewart bed" and is equivalent to localities UCLA 2312 and CSUN 374 (SQUIRES, 1984:58). Llajas Formation. Age: Early middle Eocene ("Domengine Stage"). Collectors: B. L. Clark and R. L. Squires.

UF locality Newberry Corp. Pit 1: SW ¼, SE ¼, sec. 13, T9S, R17E, Newberry quadrangle, Alachua County, northern Florida. Ocala Limestone. Age: Late Eocene. Collectors: H. S. Puri and others.

UF locality Dickerson Limerock Mines (Haile Complex): T9S, R17E, Newberry quadrangle, Alachua County, northern Florida. Inglis/Crystal River Formation. Age: Late Eocene. Collectors: D. S. Jones and students; D. Nicol and others.

UF locality Buda 1 Quarry (bed 3): NE ¼, NE ¼, sec. 32, T8S, R17E, High Springs SW quadrangle, Alachua County, northern Florida. Ocala Limestone. Age: Late Eocene. Collectors: H. S. Puri and others.

UF locality Bell Quarry (bed 6): SE ¼, NW ¼, sec. 24, R14E, T8S, Bell quadrangle, Gilchrist County, northern Florida. Ocala Limestone. Age: Late Eocene. Collectors: H. S. Puri and others.

UF locality quarry west of U.S. 441 at south edge of Kendrick: NW ¼, sec. 25, T14S, R21E, Marion County, northern Florida (NICOL & SHAAK, 1973). Crystal River Formation. Age: Late Eocene. Collectors: University of Florida, Gainesville, staff.

USGS 6812: Cummer Lumber Company, 2 km south of Newberry, Alachua County, northern Florida (MACNEIL, 1934:431). Crystal River Formation. Age: Late Eocene. Collector: C. W. Cooke.

USGS 12751: Sumter Rock Co. quarry, about 3.2 km (2 mi.) northeast of Sumterville, Sumter County, northern Florida (MACNEIL, 1934:431). Crystal River Formation. Age: Late Eocene. Collectors: W. C. Mansfield and G. M. Ponton.

Toulmin's (1977) collection, Fla-1: Mayo quarry, 7.5 km northwest of Mayo on U.S. Highway 27 and about 0.8 km south of Mayo fire tower in SE ¼, sec. 32, T4S, R11E, Lafayette County, northern Florida (TOULMIN, 1977:388). Crystal River Formation. Age: Late Eocene. Collector: L. D. Toulmin.

Nanomelon vossi, a New Deep-Water Zidoninae from Off Southern Brazil (Gastropoda: Volutidae)

by

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Abstract. *Nanomelon vossi* sp. nov. is described from the upper bathyal zone on the slope off Rio Grande do Sul State, Brazil. The new species belongs to a recently described genus, originally thought to be monotypic. It is closely related to *N. viperinus,* differing by a larger spire angle, smaller protoconch, more convex whorls, less elongate profile, larger number of spiral cords with much narrower interspaces, and flatter axial ribs in the shell. Differences in morphology of the uniserial radula are restricted to changes in the relative positions of elements and proportions of the rachidian tooth.

INTRODUCTION

The volutid genus *Nanomelon* Leal & Bouchet, 1989, originally monotypic, was recently described from deep waters off southeastern Brazil. After the publication of the description of *Nanomelon,* we realized that a small, unknown volutid, collected in 1986 on the slope off Rio Grande do Sul State, Brazil, by the Brazilian research vessel *Atlântico Sul* of the "Fundação Universidade do Rio Grande," belongs in the same genus.
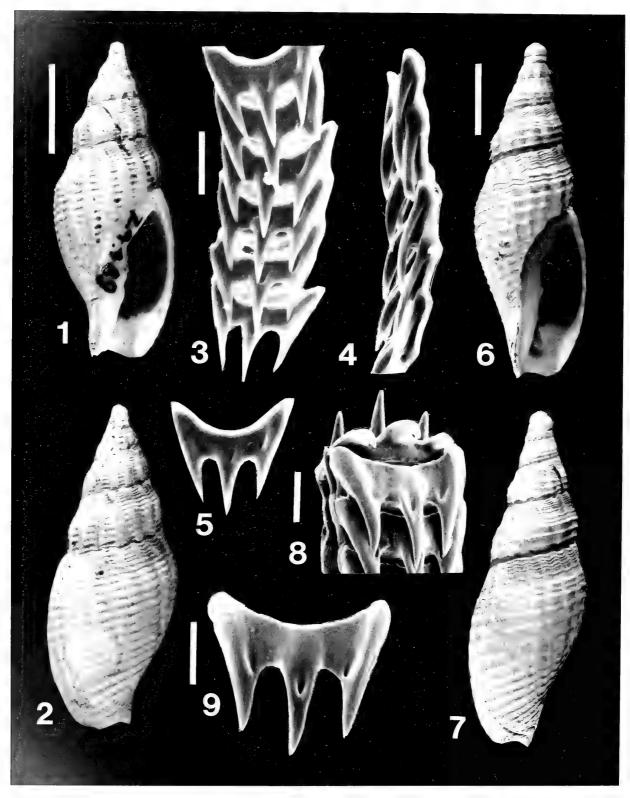
Deterioration of the soft parts due to poor preservation impeded proper anatomical comparisons with the previously described species. Notwithstanding, radular and conchological characters are distinctive enough to permit the generic allocation of the new species.

Abbreviations used in the description are as follows: MNHN, Muséum National d'Histoire Naturelle, Paris, France; MNRJ, Museu Nacional, Rio de Janeiro, Brazil; MORG, Museu Oceanográfico Prof. E. de C. Rios, Rio Grande, Brazil; USNM, National Museum of Natural History, Washington.

DESCRIPTION

Family VOLUTIDAE Rafinesque, 1815

Subfamily ZIDONINAE H. & A. Adams, 1853

Genus *Nanomelon* Leal & Bouchet, 1989

Nanomelon vossi Leal & Rios, sp. nov.

(Figures 1–5, Table 1)

Shell (Figures 1, 2, Table 1): Fusiform (length/width about 2.5), reaching 35 mm length, 13 mm width. Spire angle about 40 degrees. Shell surface opaque, dirty-white to yellowish-white. Periostracum very thin, yellowish-brown. Protoconch white, cylindrical, about 2.25 whorls, about 1.8 mm in diameter. Spiral striation adapical to suture, barely discernible. Embryonic whorl about 0.8 mm, rapidly expanding into first protoconch whorl, but last protoconch whorl with same diameter as preceding one. Teleoconch with 4.5 shouldered whorls (holotype). Suture impressed, sutural ramp slightly concave. Combination of

Explanation of Figures 1 to 9

Figures 1–5. *Nanomelon vossi* sp. nov. Figures 1, 2. Holotype, off Rio Grande do Sul, Brazil, 32°25′S, 50°11′W, 460 m depth, ventral and dorsal views of the shell. Figures 3–5. SEM micrographs of radula; anterior margin of teeth towards the top of illustration. Scale bar equals 10 mm in Figures 1 and 2. Figure 3. Radular ribbon. Figure 4. Lateral view of radular ribbon.

spiral and axial sculpture giving clathrate aspect to whole teleoconch. Spiral sculpture of 6 or 7 cordlets on sutural ramp (corresponding to adapical half of each whorl but last), and 18–23 larger spiral cords on remainder of whorl (values given for last whorl). Interspaces between cords at least twice the width of those between narrower, adapical cordlets. Spiral ribs on base not differing from those on remainder of last whorl, except for one weaker cordlet intercalated with each of 4 or 5 abapical cords. Axial ribs about 19 in last whorl. Aperture elongate (length/width about 3). Outer lip simple, thin. Interior of aperture opaque. Parietal region smooth. Columella strongly arched, with siphonal fold and 4 or 5 columellar plaits.

Radula (Figures 3–5): Radular ribbon uniserial. Rachidian 0.12 mm wide (holotype), tricuspid, basal plate strongly curved. Lateral and central cusps curved, defining planes that form respectively 10 and 20 degree angles with basal plate and radular ribbon (Figure 4). Cusps growing posteriorly from basal plate. Region of intersection of external edge of lateral cusp with anterior edge of basal plate pointed, forming well-defined angle. Central and lateral cusps with same length, but extremity of central cusp slightly more posterior than extremities of lateral cusps due to curvature of basal plate. External edges of lateral cusps forming 40 degree angle, slightly curved inwards in dorsal view. Dorsal surface of basal plate impressed by extremity of preceding teeth. Extremities of cusps interlock with these impressions in subsequent tooth, when radula not in protracted condition.

Holotype: MORG 24489, 35.1 mm length, 13.7 mm width, collected alive.

Type locality: Continental slope off the coast of Rio Grande do Sul State, Brazil, 32°25'S, 50°11'W, 460 m depth, muddy bottom, N. Oc. *Atlântico Sul,* May 1986, rectangular dredge.

Paratypes: Paratype 1, MNHN, 35.8 mm length, 14.3 mm width; paratype 2, USNM 860175, 30.3 mm length, 12.1 mm width; paratype 3, MNRJ 5767, 22.5 mm length, 9.7 mm width; all from type locality.

Etymology: The species is respectfully dedicated to the memory of the late Dr. Gilbert L. Voss and his many contributions in malacology and deep-water biology.

Remarks: Species in the genus *Nanomelon* are among the smaller ones in the subfamily Zidoninae (see WEAVER & DUPONT [1970] for dimensions of species in other genera). The small *Alcithoe grahami* (Powell, 1965) from New Zealand (about 32 mm length) was considered by DELL (1978)

Table 1

Nanomelon vossi sp. nov. Linear shell measurements and meristic counts for the holotype (Hol) and paratypes 1–3 (Pa1–Pa3). All are from the type locality, off Rio Grande do Sul State, Brazil, 32°25'S, 50°11'W, 460 m depth.

Character	Hol	Pa1	Pa2	Pa3
Total length (mm)	35.1	35.8	30.3	22.5
Shell width (mm)	13.7	14.3	12.1	9.7
Length last whorl (mm)	24.3	25.5	22.1	16.4
Aperture length (mm)	19.4	18.9	17.5	12.4
Aperture width (mm)	5.8	5.7	6.0	4.3
Protoconch diameter (mm)	1.8	—	1.8	2.0
Protoconch whorls	2.25	—	2.25	2.25
Teleoconch whorls	4.75	4.50	3.75	3.50
Spire angle (degrees)	34	39	41	40
Spiral cords last whorl	18	20	23	19
Cordlets sutural ramp	6	8	6	7
Axial ribs last whorl	19	20	13	13
Length/width	2.56	2.50	2.50	2.32
Aperture length/length	0.55	0.53	0.58	0.55
Aperture length/aperture width	3.34	3.32	2.92	2.88

to be a dwarf form of *A. wilsonae* (Powell, 1933). Poor preservation of the soft parts in *N. vossi* hampered the observation of anatomical structures used in the definition of the Zidoninae, and the present allocation is based solely on shell and radular characters.

Although only four individuals of the new species are known, adults of *Nanomelon vossi* seem on average even smaller than adults of *N. viperinus.* Both species show clathrate sculpture and a pattern of distinct, crowded spiral cordlets in the sutural ramp of whorls. *Nanomelon vossi* has a larger spire angle than *N. viperinus,* more convex whorls, and the protoconch diameter is about half of that in *N. viperinus.* As a consequence, the new species has a stubby, less elongate profile, with a more pointed apex. Cordlets and respective interspaces in the sutural ramp are not as distinctive and crowded as in *N. viperinus* and the remaining spiral cords are more numerous and interspaces much narrower in the new species. Interspaces are about three times wider than spiral cords in *N. viperinus,* but about the same width as cords in *N. vossi.* Values for the number of axial ribs in the last whorl overlap in the two species, but ribs in the new species are flatter, and the interspaces not as wide as in *N. viperinus.* Additionally, columellar and apertural regions are not as arched as in *N. viperinus.*

Differences in radular morphology are not remarkable, as expected between species of the same genus in the family

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Figure 5. Rachidian tooth. Scale bar equals 0.5 mm in Figures 3–5.

Figures 6–9. *Nanomelon viperinus* Leal & Bouchet, 1989. Holotype, off Rio de Janeiro, Brazil, 23°47'S, 42°10'W, 610 m depth. Figures 6, 7. Ventral and dorsal views of the shell. Scale bar

equals 10 mm in Figures 6 and 7. Figures 8, 9. SEM micrographs of radula; anterior margin of teeth towards the top of illustration. Figure 8. Radular ribbon. Figure 9. Rachidian tooth. Scale bar equals 0.5 mm in Figures 8 and 9. (Figures 3–5 and 9 have same magnification.)
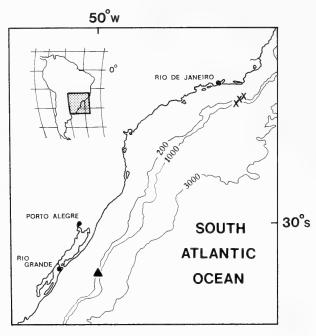
Figure 10

Records of the genus *Nanomelon*. ×, *N. viperinus*; ▲, *N.* ***vossi***. Inset shows area of South Atlantic that is detailed.

Volutidae. The angle formed by the external edges of the lateral cusps is 40 degrees in *Nanomelon* ***vossi*** and 30 degrees in *N. viperinus* and, as a result, the ratio of tooth width-distance between extremities of lateral cusps in a given tooth is larger in *N.* ***vossi***. Also, the position of the impressions in the dorsal surface of teeth is more anterior in *N.* ***vossi***, and the intersection of the external edge of the lateral cusps with the anterior margin of the tooth is well defined and pointed in *N.* ***vossi***. It is rounded and ill defined in *N. viperinus*.

The large diameter of the embryonic whorl in both species of *Nanomelon* (about 1.0 mm in *N. viperinus* and 0.8 mm in *N.* ***vossi***) and its large expansion rate indicates that, despite protoconchs with 2.5 whorls, both species exhibit non-planktotrophic, direct development. As indicated in HANSEN (1980), BOUCHET & POPPE (1988), and PENCHASZADEH (1988), this is the rule among volutids, and probably the reason for the restricted distributional range displayed by most species in the family. Records for *N. viperinus* and *N.* ***vossi*** on the slope off southeastern–southern Brazil are portrayed in Figure 10. Differences in shell morphology between the two taxa (especially the

difference in protoconch diameter and shape) and radula are here considered as sufficient to define them as distinctive species. Nonetheless, they seem to be closely related, and the geographic separation of their records on the slope suggests allopatric speciation and the recency of a common ancestor in the evolutionary history shared by the two taxa.

ACKNOWLEDGMENTS

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NOTES, INFORMATION & NEWS

New Records of Two Rare
Aeolid Nudibranchs from the
Coast of California

by

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Babakina festiva (Roller, 1972)

In its original description *Babakina festiva* was found from the coasts of California and Japan. ROLLER (1972) recorded seven specimens from the coast of California from Malibu Reef, Los Angeles County to La Jolla, San Diego County. He also recorded eight specimens from the west coast of Honshu, Japan. McDONALD (1983) recorded an additional specimen from Mantanchen, Nayarit, México, collected by Constance Boone.

On 14 June 1987, I collected a single 32-mm specimen of *Babakina festiva* from a tide pool at the Fitzgerald Marine Reserve, Moss Beach, San Mateo County. This specimen is deposited in the California Academy of Sciences as CASIZ 067110. On 14 June 1988, Marin County Parks Naturalist Bob Stewart observed a specimen of this species in the mid-intertidal zone at Duxbury Reef, Bolinas, Marin County. These collections represent the northernmost localities known for this species and the latter collection represents a range extension of approximately 480 km.

Babakina caprinsulensis Miller, 1974, was described from a single specimen collected from the North Island of New Zealand. This species differs from *B. festiva* in only a few minor regards, such as the elaboration of its rhinophores. These differences need to be verified with additional New Zealand material. It is highly likely that these two species are in fact conspecific.

Rioselleolis anadoni Ortea, 1979, was described from a single specimen from Asturias, Spain. Only its external morphology was described. Nevertheless, its known morphology is strikingly similar to *Babakina festiva*. Additional material from Spain must be collected for comparative purposes, but *R. anadoni* is likely to be a junior synonym of *B. festiva*.

Emarcusia morroensis Roller, 1972

Emarcusia morroensis was described from 32 specimens largely collected from Morro Bay, San Luis Obispo, California. The known range was from Elkhorn Slough, Monterey County, to Mission Bay, San Diego County. On 2 November 1989, I collected five specimens of this species from colonies of *Obelia* sp. attached to floating docks at the Presidio Yacht Club, Fort Baker, Marin County. The living animals were 3–15 mm in length and produced tightly coiled egg masses on the hydroid colonies. Each egg is contained in an individual capsule. These specimens are deposited in the California Academy of Sciences collections where they bear the number CASIZ 067111. These specimens represent the first record of this species since its original description.

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MILLER, M. C. 1974. Aeolid nudibranchs (Gastropoda: Opisthobranchia) of the family Glaucidae from New Zealand waters. Zool. Jour. Linn. Soc. 54:31–61.

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International Commission on Zoological Nomenclature

The following application has been published by the ICZN in the *Bulletin of Zoological Nomenclature*, volume 46, part 4, on 19 December 1989:

Case 2683: *Gryphaea pitcheri* Morton, 1834 (currently *Texigryphaea pitcheri*; Mollusca, Bivalvia): proposed conservation.

The following applications have been published by the ICZN in volume 47, part 1, on 27 March 1990:

Case 2547. Cymatiinae Iredale, 1913 (1854) (Mollusca, Gastropoda) and Cymatiinae Walton *in* Hutchinson, 1940 (Insecta, Heteroptera): proposal to remove the homonymy.

Case 2641. *Limax fibratus* Martyn, 1784, and *Nerita hebraea* Martyn, 1786 (Mollusca, Gastropoda): proposed conservation of the two specific names.

Case 2558. *Proptera* Rafinesque, 1819 (Mollusca, Bivalvia): proposed conservation.

Coments should be sent to the Executive Secretary, ICZN, % The Natural History Museum, Cromwell Road, London SW7 5BD.

Student Research Grant in Malacology

The Western Society of Malacologists and the Santa Barbara Shell Club have available grants to support student research in malacology. Funds, up to $1500, are available for actual research costs, including but not limited to, field and laboratory equipment, chemicals, photographic supplies, computer time, and travel costs. Applicant must be a full-time student in a formal graduate or undergraduate degree program, with research currently in progress or beginning in the 1990–1991 academic year.

Completed applications *must be received no later than 31 July 1990*. For information or an application, contact: Vida Kenk (408) 924-4894 or Paul Scott (805) 682-4711.

American Society of Zoologists 1990 Meeting

The 1990 meeting of the American Society of Zoologists will be held at the Marriott Rivercenter, San Antonio, Texas, from 27 to 30 December 1990. A wide variety of symposia, courses, and activities are planned.

For more information contact:
Mary Adams-Wiley, Executive Officer
American Society of Zoologists
104 Sirius Circle,
Thousand Oaks, CA 91360
(805) 492-3585

BOOKS, PERIODICALS & PAMPHLETS

Compendium of Landshells
A Color Guide to More Than 2,000
of the World's Terrestrial Shells

by R. Tucker Abbott. 1989. viii + 240 pp. American Malacologists, Inc., P.O. Box 1192, Burlington, Massachusetts 01803. Price: $56.00.

The fact that this work is offered as a compendium of *"landshells"* rather than of "land snails" or "land mollusks" is an immediate clue to its orientation. From a peak in the late nineteenth and early twentieth centuries, amateur interest in land mollusks declined after World War I. Since the 1950s it has been eclipsed by the popularity of marine shells, stimulated by SCUBA and items dredged by Asian fisheries. But something of a renaissance may be going on (it is quite possible that the trade in specimen land mollusk shells is now at an all-time high), and Abbott, the premier popularizer of malacology, addresses it with this book.

Lavishly supplied photographs tour through an astonishing diversity of form, such as the Diplommatinidae photographed in light by Robert Robertson and under SEM by Fred Thompson, and the exquisite, Venetian-glass beauty of *Turgenitubulus pagodulus.* Large, tropical species are well represented, small nondescript ones not so well. (In other words, do not expect an identification manual for the 70–80% of the world's land mollusks smaller than 10 mm.) Enough living animals are illustrated to remind us that "landshells" come, ultimately, from land snails. A 35-page bibliography, arranged geographically and taxonomically, provides a bridge to the primary literature.

The book is full of reminders that this species is extinct and that one soon may be. One of the *Compendium's* stated goals is "to awaken people to the wonders of our natural world and to encourage amateur conchologists to protect our disappearing land fauna from the inroads of pollution and habitat destruction."

The science is less than rigorously packaged and the text sometimes impeaches itself. For instance, on page 6, do, or do not, male helicinid *Viana* have a penis? With a nod in the direction of Stephen Jay Gould's studies, there are said to be "less than a dozen true species" of *Cerion* (p. 11), but later the text illustrates an even three dozen. The Baja Californian *Berendtia taylori* is placed in the Urocoptidae, although fifteen years ago, in the Abbott-edited *Nautilus,* Christensen and Miller showed it to be bulimulid. (It is correctly placed in the bibliography, p. 219.) The intertidal pulmonate limpet *Siphonaria gigas* is pictured with the caption, "Not a marine shell at all!" as if "pulmonate" and "marine shell" were mutually exclusive categories. (*Quaere*: Why are there no truly terrestrial limpets?) Page 7 repeats the old canard about the "love darts" of *Helix* being sexual stimulators, which is true in the broad sense that dart shooting is one phase of a behavioral sequence leading to copulation. However, the fine study by Chung (*The Veliger* 30(1):24–39, 1987) demonstrated that dart shooting actually *suppresses* attempts at copulation by the mate that receives the dart. Experimental biology, informed by game theory and hypotheses of sex allocation, can provide stories every bit as fascinating as the anecdotal snail lore that has come down to us through the decades.

Specialists could probably find other points to argue in their own groups. But perhaps at one level such quibbles are beside the point. Like *A Current Affair* or *The New York Post,* books that capture the popular imagination have a life and influence of their own. Would it be too cynical to suggest that, from a certain viewpoint, the fact that *Berendtia* **looks** like a urocoptid is more important than its phylogenetic affinities as revealed by dissection? In the bowels of at least one of our major museums, volunteers curate marine mollusks with Abbott and Dance's *Compendium of Seashells* open as a reference on the desk beside them. *Honi soit qui mal y pense*!

Barry Roth

Cenozoic Mollusca of New Zealand

by A. G. Beu & P. A. Maxwell, drawings by R. C. Brazier. 1990. New Zealand Geological Survey Paleontological Bulletin 58. 518 pp., 730 drawings. $140.00. (Publications Officer, New Zealand Geological Survey, PO Box 30368, Lower Hutt, New Zealand. Payable by Visa or Mastercard number.

If I were allowed to own only half a dozen malacological reference works, this would be one of them. Do not be fooled by a title that sounds paleontological and insular, and do not be discouraged by the price.

New Zealand historically has done an outstanding job of documenting the evolution of its marine molluscan fauna. Even with the tantalizing knowledge that the combined expertise of Alan Beu and Phil Maxwell were behind the project and that artist Ron Brazier had been working for 12 years on the stipple-board drawings, it was difficult to know precisely what it was that we were anticipating.

Fleming's monumental 1966 manual seemed to have the fauna so well catalogued and under such control that one would not have predicted surprising new insights. Indeed, there is nothing revolutionary about the content itself.

What is revolutionary is the form and level of scholarship. It is a manual from which one can learn and teach molluscan systematics, biostratigraphy, and evolutionary paleontology. For example, it surpasses the *Treatise on Invertebrate Paleontology* as a guide to molluscan shell morphology with a 34-page glossary (adapted from the *Treatise*) that not only defines terms but also illustrates them in a series of 38 labeled boxes of representative species. The bibliography of more than 1000 entries uses unabbreviated titles for periodicals and will provide an important bibliographic source for those who do not have large libraries or access to large libraries.

Several other resource features of the work deserve mention:

- It is unusually thoroughly indexed (53 pages of triple column entries).
- The checklist (33 pages of double-column entries of the 3200 species that have been reported from New Zealand) includes authors and dates for all taxa and stratigraphic occurrences for all species.
- There are 21 pages of biostratigraphic range charts.
- There is a separate listing of new combinations for the 216 species that are treated under new generic names, and it includes original generic allocations.

Although the work will be most exciting to those who have an interest in the biostratigraphy, paleoecology, historical biogeography, and evolution of the New Zealand mollusk fauna, there is cause for more general excitement over other aspects of the volume. Three that I single out for comment are the systematic treatments, the illustrations, and the chapter on fossil micromollusks.

The systematic paleontology is treated in 12 chapters, subdivided by age, beginning with early Paleocene faunas and concluding with those of the middle–late Pleistocene. These chapters focus on 550 key species that are described in detail and illustrated in at least one view. In addition to the large number of new generic allocations, there are careful distinctions of related taxa and helpful nomenclatural discussions.

Photographic illustration of mollusks has become standard. It may therefore seem surprising that a state-of-the-art monograph has been illustrated with drawings—but only until you have seen the plates that Ron Brazier has produced. These are high-tech drawings that record every growth line, every evidence of breakage and repair by the animal, and every taphonomic crack and preservational artifact. They are a reminder that photography is no more than an alternative technique for producing a two-dimensional image on a piece of paper, and that even a good photograph is selective in the information it conveys. They are also a rare example of attention to plate composition and balance, a matter on which students seldom receive advice, either from their mentors or from journals. Needless to say there are no tacky computer graphics or chartjunk in the monograph.

The chapter on micromollusks would stand as a substantial separate publication. It is designed as an introduction to the study of fossil micromollusks and contains detailed advice on techniques for sample preparation and specimen recovery. It is illustrated with superb scanning electron micrographs (again, the choice of method of illustration is appropriate) of representatives of 43 molluscan genera.

As a nomenclatural aside, it is pleasing to note that the authors have retained "-acea" as the superfamilial ending and not complied with the incomprehensible recommended use of "-oidea" and its invitation to confusion with the ordinal ending of "-oida."

A number of undescribed species are treated in open nomenclature, and it was exciting to recognize one that can be assigned to the heretofore endemic northeastern Pacific Eocene genus *Calliovarica* H. Vokes, 1939.

The volume is appropriately dedicated to the late Sir Charles Fleming. There is much more in this work than my review indicates. It provides an exciting new foundation for increasingly refined and detailed evolutionary understanding of what is now the world's best documented Cenozoic molluscan fauna.

Carole S. Hickman

Information for Contributors

Manuscripts

Manuscripts must be typed on white paper, 8½″ by 11″, and double-spaced throughout (including references, figure legends, footnotes, and tables). If computer generated copy is to be submitted, margins should be ragged right (*i.e., not* justified). To facilitate the review process, manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics. Metric and Celsius units are to be used.

The sequence of manuscript components should be as follows in most cases: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, figures, footnotes, and tables. The title page should be on a separate sheet and should include the title, author's name, and address. The abstract should describe in the briefest possible way (normally less than 200 words) the scope, main results, and conclusions of the paper.

Literature cited

References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Smith, 1951), for two authors (Smith & Jones, 1952), and for more than two (Smith *et al.,* 1953).

The "literature cited" section must include all (but not additional) references quoted in the text. References should be listed in alphabetical order and typed on sheets separate from the text. Each citation must be complete, with all journal titles *unabbreviated,* and in the following form:

a) Periodicals

Cate, J. M. 1962. On the identifications of five Pacific *Mitra.* The Veliger 4:132–134.

b) Books

Yonge, C. M. & T. E. Thompson. 1976. Living marine molluscs. Collins: London. 288 pp.

c) Composite works

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117–135. *In:* R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal Invertebrates of California. Stanford Univ. Press: Stanford, Calif.

Tables

Tables must be numbered and each typed on a separate sheet. Each table should be headed by a brief legend.

Figures and plates

Figures must be carefully prepared and should be submitted ready for publication. Each should have a short legend, listed on a sheet following the literature cited.

Text figures should be in black ink and completely lettered. Keep in mind page format and column size when designing figures.

Photographs for half-tone plates must be of good quality. They should be trimmed off squarely, arranged into plates, and mounted on suitable drawing board. Where necessary, a scale should be put on the actual figure. Preferably, photographs should be in the desired final size.

It is the author's responsibility that lettering is legible after final reduction (if any) and that lettering size is appropriate to the figure. Charges will be made for necessary alterations.

Processing of manuscripts

Upon receipt each manuscript is critically evaluated by at least two referees. Based on these evaluations the editor decides on acceptance or rejection. Acceptable manuscripts are returned to the author for consideration of comments and criticisms, and a finalized manuscript is sent to press. The author will receive from the printer two sets of proofs, which should be corrected carefully for printing errors. At this stage, stylistic changes are no longer appropriate, and changes other than the correction of printing errors will be charged to the author at cost. One set of corrected proofs should be returned to the editor.

An order form for the purchase of reprints will accompany proofs. If reprints are desired, they are to be ordered directly from the printer.

Send manuscripts, proofs, and correspondence regarding editorial matters to: Dr. David W. Phillips, Editor, 2410 Oakenshield Road, Davis, CA 95616 USA.

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THE

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CONTENTS — *Continued*

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

Reproductive, Morphological, and Genetic Evidence for Two Cryptic Species of Northeastern Pacific *Nucella*

by

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Abstract. Laboratory crosses among four geographically distant populations of the northeastern Pacific, rocky shore gastropod *Nucella emarginata* (=*Thais emarginata*) (Deshayes, 1839) yielded evidence of reproductive isolation between "northern" and "southern" populations. Although between-population crosses with individuals from Torch Bay (Alaska), Bamfield (British Columbia), and San Juan Island (Washington) yielded viable F1 and F2 offspring, those between-population crosses involving individuals from Santa Barbara (California) yielded only capsules whose eggs did not develop. The success of within-population crosses for all four populations confirmed that this inability to reproduce was not a laboratory artifact. Northern and southern populations also differed in egg-capsule morphology (northern—vase shaped; southern—rolling-pin shaped) and in the form of spiral sculpture (northern—uniform spiral ribs; southern—regularly spaced knobs along the spiral ribs). Finally, a survey of allozyme variation revealed fixed allelic differences at one locus, and a genetic distance estimate (*D*) of 0.16, between two nearly sympatric populations separated by less than 500 m in central California. Collectively, these data suggest very strongly that northern and southern populations currently referred to *N. emarginata* actually belong to two reproductively isolated cryptic species.

INTRODUCTION

Because of their highly variable shells, thaidine gastropods from the northeastern Pacific have a colorful taxonomic history. Among the four currently accepted species, DALL (1915) listed no less than nine synonyms for *Nucella lamellosa*, five synonyms for both *N. lima* and *N. canaliculata*, and four for *N. emarginata*. In contrast, in apparent frustration because of their variable shells, TRYON (1880) had previously lumped all the currently recognized species of *Nucella* from the northern hemisphere into a single, geographically widespread species, *Nucella lapillus* [as *Purpura*]: " The quantity and variety of material before me, embracing a rich series of forms from many localities, together with the comparison of numerous descriptions and figures that have been published, induce me to include under this, the oldest name, a very large number of nominal species. . . . I have considered it preferable to retain some of these names as indicating growth modifications and localities; those who take a more conservative view than myself will thus have the names and descriptions at hand to designate these several forms as varieties or species, or even genera, if it so pleases them." More recently, KINCAID (1964) lumped the nominal species *canaliculata*, *emarginata*, and *lima* into the single species *Nucella lima*, because he considered their shells to intergrade. Clearly, traits other than shell form are required to distinguish among these and related species.

Each of the four currently recognized species of *Nucella* from the northeastern Pacific appears to have a wide geographic range (ABBOTT, 1974; PALMER, 1984a). Although some of these reported ranges are incorrect (VERMEIJ *et al.,* 1990), each species occurs over at least 5000 km of

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coastline. Furthermore, all four species lack a planktonic larval stage: crawl-away hatchlings emerge directly from the egg capsule (STRATHMANN, 1987). These wide geographic ranges, coupled with the presumably limited gene flow associated with the lack of pelagic larvae, should promote genetic divergence. Whether such divergence would be sufficient to result in reproductive isolation depends on its form and extent.

Low levels of gene flow do appear to have promoted local genetic differentiation in *Nucella lamellosa*. For example, GRANT & UTTER (1988) observed significantly different allozyme frequencies among populations on the scale of meters to hundreds of kilometers. However, based upon a survey of allozyme variation among 12 populations ranging from Glacier Bay, Alaska, to San Francisco, California, CAMPBELL (1978) concluded that in spite of extensive differences "there is no reason to assign the populations subspecific, racial or ecotypic status." Nonetheless, by themselves, differences in allozyme frequencies over large geographic distances reveal little about the potential viability or fecundity of hybrids, and hence provide at best a coarse estimate of a species' status.

When hybrid crosses are inviable, a convincing case can be made for cryptic species. Such crosses, however, are often difficult and time consuming, and do not permit many populations to be examined. Furthermore, reproductive isolation observed between geographically distant populations could result from isolation by distance (WRIGHT, 1943) or reflect the presence of two discrete species. In such a situation, a combination of genetic, ecological, and morphological variation among intervening populations would help delineate more clearly between these two alternatives. We present such evidence here.

COLLECTION SITES AND PROCEDURES

Reproductive Isolation and Morphological Variation

To test for reproductive isolation, individuals of *Nucellla emarginata* were collected from four sites along the Pacific coast of North America:

(I) TORCH BAY, ALASKA (code = AK)—the bedrock shores at the mouth of the west arm (58°19'41"N, 136°47'56"W), on the outer coast of the Glacier Bay National Monument in both July 1980 and July 1982,

(II) BAMFIELD, BRITISH COLUMBIA (code = BC)—the north shore of Wizard Id. (48°51'30"N, 125°09'33"W), near the Bamfield Marine Station on the west coast of Vancouver Id. in August 1980 and December 1981,

(III) SAN JUAN ISLAND, WASHINGTON (code = WA)—from among boulders on the north shore of Cattle Pt. (48°27'42"N, 122°58'58"W), 2–300 m E of the mouth of Jaekel's Lagoon in May 1981, and

(IV) SANTA BARBARA, CALIFORNIA (code = CA)—from the rocks of Coal Oil Pt. (34°23'N, 119°42'W), near the UCSB campus in December 1981.

Both within- and between-population crosses were initiated with field-collected animals. Snails were sexed and maintained in the laboratory as described in PALMER (1985a). Cages were checked for egg capsules every two to four weeks. Crosses were monitored for 12 to 34 months (mean = 18.9 months). All surviving parents from between-population crosses involving California snails were subsequently re-paired with snails from their source population to verify that they were fertile. These crosses were held and monitored as above for 13 to 23 months (mean = 17.4 months).

In any such study of reproductive isolation, the possibility that field-collected females store sperm must be addressed, particularly in gastropods where sperm may be stored for periods up to 12 months or more (ANSELL, 1982; FRETTER & GRAHAM, 1962). Except where noted, the 55 initial crosses in the present study were begun with immature snails (males: 16.7 ± 3.11 mm; females: 17.0 ± 3.14 mm; mean shell length $\pm$ SD, $n = 47$ both sexes). In six of the eight crosses started with mature female snails, at least six months were allowed to pass before egg capsules were collected (see Table 2a, b below) to allow for loss of stored sperm (PALMER, 1985a, and unpublished). In the remaining two crosses with mature female snails, capsules were collected less than six months after initiation (82-47, 82-49), but these capsules were saved specifically as part of a sperm-storage study using color markers. In both these cases, sperm from prior mating was no longer present after the first three clutches had been laid, and most subsequent clutches (five and six, respectively) were viable. In the fertility-test crosses, all the mature females were those from crosses in which none of the egg capsules yielded viable embryos; hence, stored sperm was not a consideration.

To determine the geographic distribution of distinctive features of spiral sculpture and egg-capsule morphology, snails and egg capsules were collected from more than 20 sites along the Pacific coast from Bamfield, BC, to Santa Barbara, California, in April and May 1985 (see Figure 3 below). An additional collection was made at Crystal Cove, California, in February 1990.

Allozyme Variation

Allozyme variation was examined in samples collected in April 1986 from five central California sites. These sites spanned the region where northern and southern forms of spiral sculpture and egg-capsule morphology appeared to overlap. One additional sample from Bamfield, collected in June 1986, was also analyzed for comparison with the California samples. Samples were collected as follows (from north to south):

BAMFIELD (48°50'04"N, 125°08'47"W)—from a continuous bedrock shore at the S end of Scott's Bay, near the Bamfield Marine Station (moderately exposed),

BODEGA HEAD (38°18'N, 123°04'W)—from the rocks near the southernmost tip (very exposed),

BODEGA BAY HARBOR (38°19′N, 123°03′W)—from among rock and concrete rubble along the W side of the channel inside the breakwater (very protected),

FORT PT. (37°49′N, 122°28′W)—from the boulders and seawall just E of the S end of the Golden Gate Bridge, San Francisco (moderately exposed),

PILLAR PT. (37°30′N, 122°30′W)—from a bedrock bench at the N end of Halfmoon Bay, approximately halfway from the base of the cliffs to the outermost rocks (exposed), and

HALFMOON BAY HARBOR (37°29′N, 122°24′W)—from rocks and debris along the otherwise sandy north shore of the harbor inside the breakwater (very protected).

These samples of 20 to 50 snails were frozen and sent to UCSD where they were stored at −70°C until electrophoresed. In preparation for electrophoresis, individuals were thawed, and the head-foot tissue was quickly separated from the digestive tissue and placed in Eppendorf tubes on ice. Chilled distilled water (0.1 mL) was added to the tubes and the tissues were homogenized with a glass rod. The homogenate was then centrifuged for 2 min at 10,000 g, and the supernatant absorbed onto 3 × 9 mm wicks of Whatman No. 3 chromatography paper. The wicks were blotted and loaded into chilled horizontal 12% starch (Sigma Chemical Co., St. Louis, Missouri) gels. The electrophoretic procedures followed those of WOODRUFF (1975) and MULVEY & VRIJENHOEK (1981). The particular buffer used for each of the 11 examined enzyme systems depended upon the enzyme (Table 1). At least two samples were included on each gel, the arrangement of which was varied to permit informative comparisons about the relative mobilities of alleles from different populations. Isozymes were assigned Roman numerals, and allozymes assigned values corresponding to their relative mobility (relative to the common allele in Bamfield) in order of decreasing mobility toward the anode.

The electrophoretic data were analyzed using BIOSYS-1 (SWOFFORD & SELANDER, 1981). Chi-square and Fisher exact tests for Hardy-Weinberg equilibrium were employed to examine the assumption of panmixia. The genetic structure of the population was examined using WRIGHT's (1978) hierarchical F-statistics. NEI's (1978) unbiased genetic distance and ROGERS' (1972) genetic similarity were calculated and clustered using the UPGMA algorithm.

RESULTS

Within- and Between-Population Crosses

Except for the occasional cross, all within-population crosses produced at least one clutch, and most yielded several (Table 2a). In only 3 of these 36 crosses did capsules contain infertile eggs, and each was initiated with snails from a different source population. The average percentage of clutches that hatched ranged from 89 to 100% among the four source populations (Figure 1a).

Table 1

Buffers used to resolve protein variation in *Nucella emarginata.*

Enzyme (EC No.)	Abbreviation	Buffer†
Aspartate aminotransferase (2.6.1.1)	*Aat*	TBE 8.0
Esterase (1.11.1.6)	*Est*	LiOH
Glucose phosphate isomerase (5.3.1.9)	*Gpi*	TBE 8.0
Glucose-6-phosphate dehydrogenase (1.1.1.49)	*G6pd*	TC 6.8
Isocitrate dehydrogenase (1.1.1.42)	*Idh*	TC 6.8
Malate dehydrogenase (1.1.1.37)	*Mdh*	TC 6.8
Malic enzyme (1.1.1.40)	*Me*	TBE 8.0
Peptidase$_{la}$ (3.4.11)	*Pep$_{la}$*	LiOH
Peptidase$_{lgg}$ (3.4.11)	*Pep$_{lgg}$*	TBE 9/8
Phosphoglucomutase (2.7.5.1)	*Pgm*	TBE 9/8
Sorbitol dehydrogenase (1.1.14)	*Sordh*	LiOH

† TC 6.8: 0.188 M Tris, 0.065 M citrate, pH 6.8; diluted 1:10 for gels and 1:5 for electrodes (running time 18–21 hr at 150 V). TBE 8.0: 0.5 M Tris, 0.065 M borate, 0.02 M EDTA, pH 8.0; undiluted (18–21 hr, 80–100 V). TBE 9/8: 0.087 M Tris, 0.086 M borate, 0.001 M EDTA, pH 9.0; diluted 1:3 for gels. 0.5 M Tris, 0.065 M borate, 0.02 M EDTA, pH 8.0; undiluted for electrodes (17–21 hr, 80 V). LiOH: Solution A—0.03 M LiOH, 0.19 M borate, pH 8.1; Solution B—0.008 M citrate, 0.05 M Tris, pH 8.4; 10% A plus 90% B for gel, undiluted A for electrodes (18–22 hr, 120–150 V).

Between-population crosses involving one parent from California yielded evidence of reproductive isolation. Only two of 19 between-population crosses failed to produce any egg capsules at all, and both were BC × WA crosses initiated with mature females (Table 2b). Of those between-population crosses that did produce egg capsules, however, with one exception, the only crosses that failed to yield viable embryos involved one parent from California (crosses 82-32 to 82-38, Table 2b; Figure 1b). The one exception was an AK × BC cross (80-12), but all the clutches of the remaining seven AK × BC crosses developed normally.

When surviving parents of crosses involving one California snail (82-32 to 82-38) were re-paired with those from their native population, all produced additional capsules (Table 2c). Significantly, all of these crosses, which included parents from Alaska, British Columbia, and California, yielded egg capsules with fertile embryos (Figure 1c). Furthermore, in all but one instance, 100% of the clutches were viable (Table 2c).

Variation in Egg-Capsule Morphology and Shell Sculpture

Snails from the northern populations used in the hybridization experiments produced egg capsules whose shape differed from those of the California population. Typically, capsules produced by snails from Alaska and British Columbia were more vase shaped with a proportionally lon-

Table 2

Outcome of crosses within and among four widely separated populations of *Nucella emarginata* along the Pacific Coast of North America. AK = Torch Bay, Alaska, BC = Bamfield, British Columbia, CA = Santa Barbara, California, WA = San Juan Island, Washington. See methods and Figure 4 for exact locations. Dates are Month/Day/Year. Date of first clutch refers to the date on which egg capsules were first noted.

Group	Cross label	Male Source	Male Size (mm)	Female Source	Female Size (mm)	Date cross initiated (m/d/y)	Time to first clutch (mo)	Duration of cross (mo)	Clutches n	Clutches % hatched	Ave. no. capsules per clutch	Ave. no. clutches per mo of laying
a) Original within-population crosses												
AK	80-15	AK	12.4	AK	12.4	9/2/80	7.0§	16.1	3	100	14.7 ± 9.45	0.33
	80-16	AK	12.0	AK	14.2	9/2/80	6.0§	16.1	3	100	16.7 ± 0.58	0.30
	82-55	AK	19.8	AK	16.9	9/6/82	7.0	20.3	6	100	8.7 ± 4.89	0.45
	82-56	AK	19.8	AK	18.1	9/6/82	7.0	16.2	2	100	14.5 ± 9.19	0.22
	82-57	AK	19.6	AK	20.3	9/6/82	6.3	16.2	4	100	8.5 ± 3.79	0.40
	82-58	AK	21.2	AK	19.8	9/6/82	6.5	25.6	3	100	13.3 ± 2.08	0.16
	82-59	AK	20.2	AK	19.8	9/6/82	6.1	17.8	3	100	12.7 ± 3.21	0.26
	82-60	AK	16.3	AK	20.2	9/6/82	7.0	16.2	1	100	5 —	0.11
	82-61	AK	16.5	AK	18.8	9/6/82	5.9	17.8	5	100	11.6 ± 5.18	0.42
	82-62	AK	17.8	AK	23.0	9/6/82	5.9	20.8	6	100	13.3 ± 3.01	0.40
	82-63	AK	19.0	AK	15.2	9/6/82	13.4	24.5	1	?	2 —	0.09
	82-64	AK	19.4	AK	18.3	9/6/82	19.7	30.0	2	100	8.5 ± 2.12	0.19
	82-65	AK	22.6	AK	20.3	9/6/82	7.0	20.3	2	100	6.5 ± 0.71	0.15
	82-66	AK	18.8	AK	21.8	9/6/82	9.6	33.9	5	80	8.8 ± 3.42	0.21
	82-67	AK	19.8	AK	21.5	9/6/82	7.0	17.8	3	100	14.7 ± 6.03	0.28
	82-68	AK	15.8	AK	19.8	9/6/82	6.1	17.8	3	100	9.7 ± 2.89	0.25
	82-69	AK	19.2	AK	16.2	9/6/82	7.7	24.5	2	100	9.0 ± 1.41	0.12
	82-70	AK	20.3	AK	20.1	9/6/82	7.5	17.1	2	100	12.5 ± 6.36	0.21
BC	80-17	BC	14.0	BC	13.6	9/2/80	3.0§	16.1	6	100	16.3 ± 6.65	0.46
	80-18	BC	12.3	BC	12.2	9/2/80	3.0§	16.1	8	100	13.1 ± 5.28	0.61
	82-25	BC	14.6	BC	18.0	2/24/82	7.3†	14.9	4	100	12.5 ± 3.11	0.53
	82-26	BC	16.8	BC	16.0	5/9/82	7.3	16.2	9	100	8.4 ± 4.22	1.00
	82-27	BC	15.4	BC	18.5	1/1/82	9.1†	20.5	6	100	12.2 ± 3.19	0.53
	82-28	BC	16.3	BC	19.5	1/1/82	6.4†	20.5	10	100	13.4 ± 3.37	0.71
	82-51	BC	17.5	BC	13.2	6/15/82	6.0	14.7	7	0	12.6 ± 4.08	0.81
	82-52	BC	12.2	BC	16.0	6/15/82	7.7	19.0	5	100	10.6 ± 2.70	0.44
	82-53	BC	12.3	BC	12.7	6/15/82	8.6	19.0	3	100	8.0 ± 1.00	0.29
WA	82-40	WA	18.0	WA	18.4	6/10/82	5.1	15.2	6	100	13.2 ± 4.67	0.60
	82-41	WA	18.6	WA	27.9*	6/10/82	7.6	14.9	3	0	12.3 ± 3.21	0.41
	82-42	WA	15.6	WA	17.2	6/10/82	5.8	20.8	3	100	17.7 ± 14.0	0.20
	82-43	WA	18.0	WA	16.9	6/10/82	9.9	22.6	4	75	12.3 ± 6.70	0.31
	82-44	WA	14.9	WA	20.1	6/10/82	8.8	20.8	1	100	12 —	0.08
	82-45	WA	16.6	WA	17.7	6/10/82	6.2	19.1	6	100	15.7 ± 7.12	0.46
	82-46	WA	21.8*	WA	19.6	6/10/82	6.2	15.2	5	100	12.8 ± 5.26	0.56
CA	82-30	CA	21.9*	CA	19.9*	2/25/82	9.7	18.7	8	100	12.8 ± 2.49	0.89
	82-31	CA	18.4*	CA	25.3*	2/25/82	7.5†	17.0	3	100	14.7 ± 3.79	0.31

Table 2

Continued.

| | | Parents | | | | | Time to | Duration | Clutches | | Ave. no. | Ave. no. |
| | | Male | | Female | | Date cross | first | of cross | | | capsules | clutches per mo |
Group	Cross label	Source	Size (mm)	Source	Size (mm)	initiated (m/d/y)	clutch (mo)	(mo)	n	% hatched	per clutch	of laying
b) Original between-population crosses												
AK × BC	80-01	AK	12.9	BC	13.7	9/2/80	3.0§	21.7	9	100	16.2 ± 6.42	0.48
	80-02	AK	12.3	BC	15.2	9/2/80	3.0§	21.7	9	100	17.9 ± 8.92	0.48
	80-03	BC	14.1	AK	16.3	9/2/80	3.0§	16.1	5	100	11.8 ± 6.69	0.38
	80-04	BC	14.5	AK	14.2	9/2/80	7.0§	21.7	5	100	14.2 ± 7.50	0.34
	80-11	AK	11.9	BC	11.7	9/2/80	3.0§	21.7	10	100	15.4 ± 4.45	0.54
	80-12	AK	13.7	BC	14.0	9/2/80	3.0§	21.7	6	0	16.0 ± 6.00	0.32
	80-13	BC	14.0	AK	15.0	9/2/80	7.0§	16.1	2	100	26.0 ± 2.83	0.22
	80-14	BC	12.2	AK	13.5	9/2/80	7.0§	21.7	3	100	12.3 ± 5.86	0.21
AK × CA	82-32	CA	19.9*	AK	24.0	2/25/82	13.9	18.7	2	0	9.0 ± 8.49	0.42
	82-33	CA	21.2*	AK	19.6	2/25/82	13.4	18.7	2	0	16.0 ± 11.3	0.38
	82-34	CA	16.1	AK	13.9	2/25/82	14.4	18.7	2	0	5.5 ± 2.12	0.47
	82-35	AK	23.2	CA	12.5	2/25/82	—	18.7	0	—	—	—
BC × WA	82-47	BC	20.8	WA	26.3*	6/10/82	2.0	15.2	8	88	13.8 ± 6.80	0.61
	82-48	BC	19.2	WA	26.8*	6/10/82	—	11.6	0	—	—	—
	82-49	BC	22.9*	WA	26.1*	6/10/82	1.3	15.2	9	78	13.1 ± 5.01	0.65
	82-50	BC	19.2	WA	28.5*	6/10/82	—	11.6	0	—	—	—
BC × CA	82-36	CA	21.5*	BC	14.5	2/25/82	7.5†	18.7	10	0	12.4 ± 6.33	0.90
	82-37	CA	20.4*	BC	14.7	2/25/82	7.5†	18.7	6	0	13.8 ± 7.00	0.54
	82-38	BC	17.7	CA	19.0*	2/25/82	7.5†	18.7	11	0	14.1 ± 4.32	0.99
c) Fertility tests of snails used in between-population crosses involving California parents												
AK	83-22	82-35‡	29.8*	82-32	28.8*	9/8/83	2.5	18.4	3	100	8.7 ± 9.07	0.19
	83-23	AK	28.8*	82-33	27.0*	9/8/83	8.1	13.3	2	100	9.0 ± 4.24	0.38
	83-24	AK	28.1*	82-34	27.8*	9/8/83	6.9	22.6	4	25	5.0 ± 3.16	0.25
BC	83-20	BC	14.2	82-36	28.5*	9/8/83	3.0	13.9	6	100	8.8 ± 6.77	0.55
	83-21	82-38	27.7*	82-37	29.1*	9/8/83	3.7	13.6	7	100	9.6 ± 5.09	0.70
CA	83-25	82-37	25.1*	82-38	27.9*	9/8/83	2.8	17.8	8	100	12.9 ± 5.87	0.53
	83-26	82-33	24.2*	CA	15.2	9/8/83	—	6.8	0	—	—	—
	83-27	82-34	26.4*	CA	18.1	9/8/83	8.6	22.2	3	100	13.3 ± 9.61	0.22
	83-28	82-36	30.6*	CA	16.6	9/8/83	—	8.7	0	—	—	—

* Mature parent.
§ Estimated from apparent age of capsules.
† Estimated ± 30 days.
‡ Number of between-population cross in which parent was originally used.
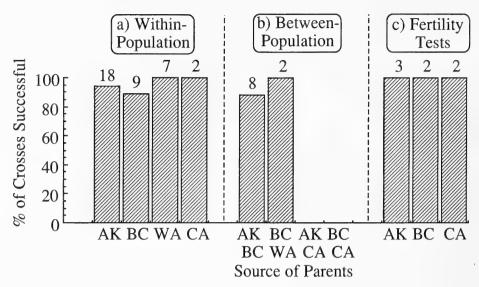
Figure 1

Percent of within- and between-population crosses with *Nucella emarginata* that were successful (*i.e.,* yielded at least some egg capsules with viable embryos; see Table 2) for parents originating from four different populations. Origins of parents: AK—Torch Bay, Alaska; BC—Bamfield, British Columbia; WA—San Juan Island, Washington; CA—Santa Barbara, California (see methods and Figure 4 for exact locations). Numbers above bars equal number of crosses; $n = 3$ for AK × CA and BC × CA.

ger neck (Figure 2a, b) compared to those from the California population. Capsules from the California parents were much more cylindrical and had a proportionally shorter neck that was often flared distally (Figure 2d). These differences in egg-capsule morphology were also used to identify parapatric populations of the putative "northern" and "southern" forms (Figure 2c and 2e, respectively) to test for gene flow using protein electrophoresis.

In addition, the form of spiral sculpture differed consistently between populations north and south of the San Francisco Bay area. Where sculpture was well developed, northern populations produced spirally uniform ribs (Figures 3, 4), although crenulations and growth checks sometimes caused minor, irregular variations in rib height. In southern populations, however, where sculpture was prominent it always included regularly spaced knobs along the distal margin of the spiral ribs (Figures 3, 4). Unfortunately, no consistent differences in shell shape were observed between populations north and south of the San Francisco Bay area. Therefore, in populations from wave-exposed shores where spiral sculpture was very weakly developed or absent, shells could not be identified reliably as "northern" or "southern."

Allozyme Variation

Consistent and genetically interpretable results were obtained for 18 loci from all samples (Tables 3, 4). In all six populations the mean number of alleles per locus (*A*) ranged from 1.1 to 1.2. The percentage of polymorphic

loci (*P*) varied from 10.5 to 21.1% (loci were considered polymorphic if more than one allele was detected). Mean individual heterozygosity (*H*; by direct count) ranged from 0.009 to 0.041.

Only a few samples appeared to depart from panmixia. Among the 23 chi-square tests involving polymorphic loci (Table 3), 20 met Hardy-Weinberg expectations ($p >$ 0.05). Only one locus at each of three sites did not: the *Aat-1* locus from Bamfield ($p = 0.033$), the *Lap-1* locus from Bodega Head ($p = 0.004$), and the *Lap-1* locus from Bodega Harbor ($p = 0.009$). Three significant results out of 23 independent chi-square tests were only slightly higher than that expected due to chance. Wright's *F*-statistics for all loci revealed a departure from panmixia ($F_{IS} =$ 0.188), largely due to variation at the *Aat-1, Lap-1,* and *Pgm-2* loci. We are presently unable to account for these results as our sampling was not designed to address such questions. Pooling of different year classes may have contributed to this heterogeneity.

Cluster analysis of multilocus genetic-distance measures between the different populations (Table 5, Figure 5) revealed that the Bodega Head and Bodega Harbor populations were nearly identical, as were those from Pillar Pt. and Fort Pt. These four California populations were also closely related to each other with a genetic distance of $D = 0.01$, and were all moderately differentiated from the Bamfield population with a mean distance of $D = 0.11$. In contrast, the five northern populations differed considerably from the Halfmoon Bay population, with a mean genetic distance of $D = 0.20$ (Figure 5).

Figure 2
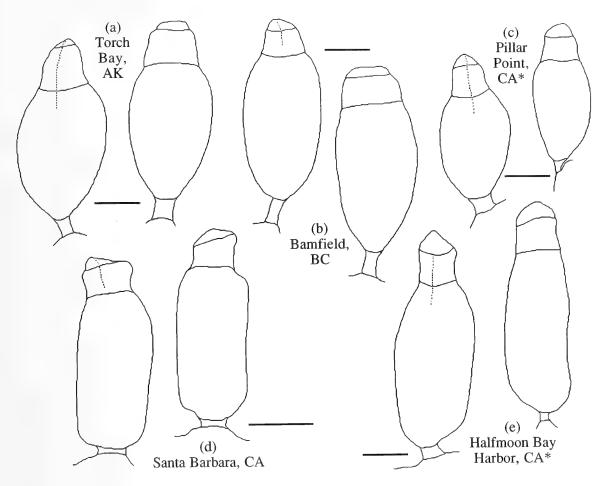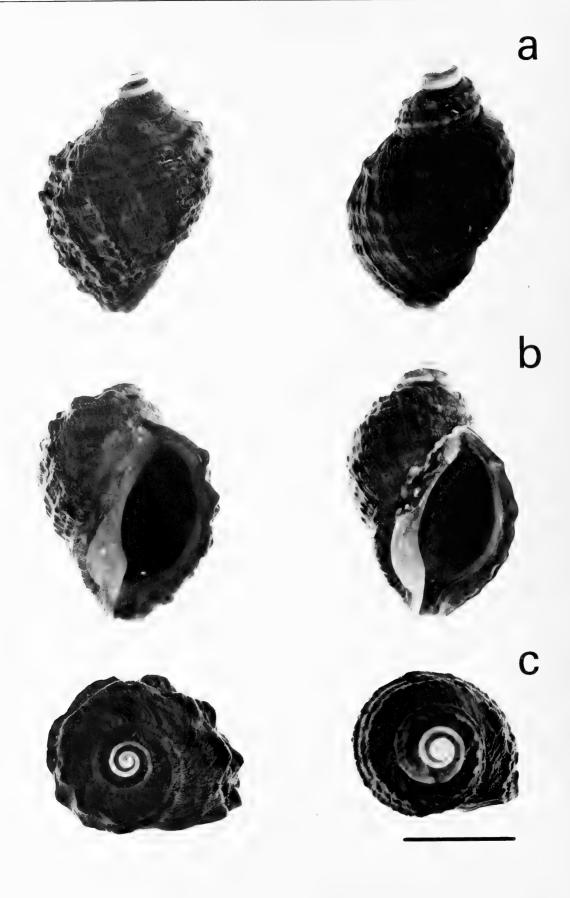
Camera lucida drawings of egg capsules from five populations of *Nucella emarginata* (see methods and Figure 4 for exact locations). Two views of an individual, representative capsule are illustrated for each population: a seam view (dotted line along neck) and a view perpendicular to the plane of the seam. Capsules (a), (b), and (d) were laid in the laboratory and (c) and (e) were collected from the field. Capsules (a)–(c) illustrate the "northern" form and capsules (d) and (e) illustrate the "southern" form. Scale bars = 2 mm (capsules not all drawn to same scale). *Note that (c) and (e) were collected from populations less than 500 m from each other.

The Halfmoon Bay population differed genetically from the remaining populations examined in several other important respects, even though this population was less than 500 m from the Pillar Pt. sample. First, it exhibited fixed allelic differences at one of the eight loci exhibiting more than one allele (*Idh-2*). Second, at two of the remaining seven loci (*Aat-1* and *Pep*$_{la}$*-2*), a unique allele was observed at moderate to high frequency in the Halfmoon Bay population. Third, even with allozyme data included for the population from Bamfield, BC, some 1600 km to the north, the Halfmoon Bay population was the most genetically distinct of all those examined (Figure 5). These genetic differences between the Halfmoon Bay and the nearby Pillar Pt. populations, when coupled with the differences in egg-capsule morphology (Figure 2), suggest very strongly an absence of gene flow between the northern and southern cryptic species.

DISCUSSION

Reproductive Isolation

Four lines of evidence suggest that complete reproductive isolation has evolved between central Californian and northeastern Pacific populations of the species currently recognized as *Nucella emarginata*. First, the only crosses that consistently yielded egg capsules whose embryos did not develop were hybrid crosses between Californian and northern populations (Table 2b, Figure 1b). The infertile capsules produced by these crosses were important evidence because they showed that neither laboratory conditions nor lack of a suitable mate inhibited capsule production. Inviable egg capsules were produced in a few other crosses (3 of 37 within-population [Table 2a], and 1 of 10 between-population crosses [Table 2b]), but no more than

a

b

c
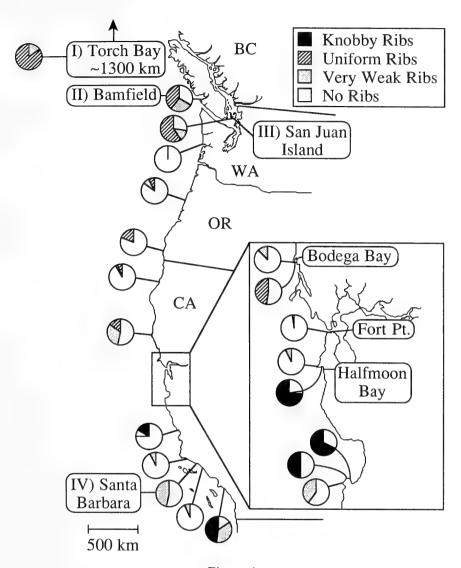
Figure 4

Frequencies of different forms of spiral sculpture in populations of *Nucella emarginata* from the west coast of North America. Sites preceded by Roman numerals indicate populations used to assess reproductive isolation (see Table 2 and Figure 1). Solid sections—regularly spaced knobs present on spirally sculptured individuals; cross-hatched sections—no regularly spaced knobs evident on spirally sculptured individuals; stippled sections—sculpture present but too weak to identify as uniform or knobby; open sections—smooth-shelled individuals. Sample sizes ranged from 13 to 191 (median *n* = 37).

Figure 3

Forms of spiral shell sculpture for the southern form (left, Halfmoon Bay), and northern form (right, Grappler Inlet, Vancouver Island, British Columbia, 48°49′54″N, 125°07′00″W) of *Nucella emarginata*. Note the prominent, regularly spaced knobs along the ribs of the southern form. a, abapertural view; b, apertural view; and c, apical view. These shells, along with others from the same site, have been deposited in the Los Angeles County Museum (accession numbers 86-449.1 and 86-448.2 for the southern and northern forms, respectively). Scale bar = 10 mm. Egg capsules for the "northern" and "southern" species have been similarly deposited (accession numbers 86-447.1 and 86-448.1, for Bodega Bay Harbor and Halfmoon Bay Harbor respectively).
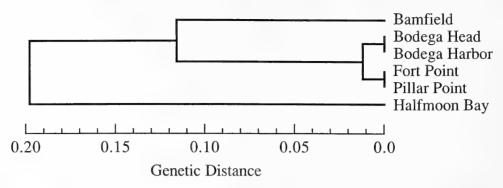
Figure 5

Phenetic tree of multilocus similarities among five populations of *Nucella emarginata* based on UPGMA clustering of Nei's (1978) genetic distances (see methods and Figure 4 for exact locations of samples).

Table 3

Sample sizes, and allele frequencies of allozyme variants, for six populations of *Nucella emarginata*† (see methods and Figure 4 for exact locations).

Locus/ Allele RM*	Population					
	Bam-field	Bodega Head	Bodega Harbor	Fort Point	Pillar Point	Half-moon Bay
Aat-1	25§	11	14	14	15	29
100	0.62	0.50	0.50	0.07	0.03	0.0
86	0.38	0.50	0.50	0.93	0.97	0.62
71	0.0	0.0	0.0	0.0	0.0	0.38
Idh-1	40	20	20	15	15	30
106	0.0	0.03	0.0	0.0	0.0	0.0
100	1.0	0.97	1.0	1.0	1.0	1.0
Idh-2	40	20	18	15	15	30
109	0.0	0.0	0.0	0.0	0.0	1.0
100	1.0	1.0	1.0	1.0	1.0	0.0
Lap-1	31	15	17	4	10	23
100	1.0	0.33	0.32	0.13	0.20	0.02
90	0.0	0.67	0.68	0.87	0.80	0.98
Pep$_{la}$-2	40	20	20	15	15	30
100	1.0	0.03	0.03	0.0	0.0	0.0
85	0.0	0.97	0.97	1.0	1.0	0.05
38	0.0	0.0	0.0	0.0	0.0	0.95
Pep$_{lgg}$	40	15	15	10	10	30
100	0.60	0.97	0.87	0.90	0.85	0.02
97	0.0	0.03	0.13	0.10	0.15	0.98
95	0.40	0.0	0.0	0.0	0.0	0.0
Pgm-2	30	20	20	15	15	20
105	0.17	0.0	0.0	0.0	0.0	0.0
100	0.83	1.0	1.0	1.0	1.0	1.0
Sordh	35	10	10	10	10	25
100	0.97	1.0	1.0	1.0	1.0	1.0
82	0.03	0.0	0.0	0.0	0.0	0.0

† Monomorphic loci: *Aat-2, Est, Gpi, Lap-2, Ldh, Mdh-1, Mdh-2, Me, Pep$_{la}$-1, Pgm-1.*

* RM: relative mobility, decreasing toward anode.

§ Number of individuals.

one instance of such infertility occurred within any category of cross. Therefore, no category of cross was particularly susceptible to infertility.

Second, with few exceptions, all within-population crosses from the four populations examined yielded egg capsules with viable embryos (Table 2a, Figure 1a); hence mating itself was not inhibited in the laboratory. Third, and most significantly, when parents originally present in between-population crosses involving California snails were re-paired with snails from their source population, they produced capsules whose embryos developed normally (Table 2c, Figure 1c). Hence the lack of fertile capsules in the rather small number of these initial between-population crosses was not just due to a chance lack of fertility among the parents. Without additional information, we unfortunately cannot determine how reproductive isolation was achieved. It may have occurred before or after mating.

Finally, although the distance between Santa Barbara, California, and Bamfield, British Columbia (ca. 1800 km) is comparable to that between Bamfield and Torch Bay,

Table 4

Mean sample size per locus (*n*), mean number of alleles per locus (*A*), percentage of loci polymorphic (*P*), and average number of heterozygous loci per individual (*H*, by direct count) for six populations of *Nucella emarginata* analyzed for allozyme variation (computed from data in Table 3).

Population	*n*	*A*	*P*	*H*
Bamfield	36.6	1.2	21.1	0.041
Bodega Head	18.4	1.2	21.1	0.017
Bodega Harbor	18.4	1.2	15.8	0.022
Fort Pt.	13.4	1.1	10.5	0.024
Pillar Pt.	13.7	1.2	10.5	0.037
Halfmoon Bay	25.9	1.2	15.8	0.009

Table 5

Genetic similarity and genetic distance estimates among six populations of *Nucella emarginata* from the Pacific Coast of North America. Above diagonal: NEI's (1978) unbiased genetic distance. Below diagonal: ROGERS' (1972) genetic similarity.

Population	1	2	3	4	5	6
1 Bamfield	—	0.145	0.148	0.187	0.182	0.313
2 Bodega Head	0.828	—	0.000	0.010	0.012	0.184
3 Bodega Harbor	0.829	0.992	—	0.010	0.011	0.173
4 Fort Pt.	0.794	0.959	0.964	—	0.000	0.164
5 Pillar Pt.	0.797	0.958	0.967	0.991	—	0.162
6 Halfmoon Bay	0.712	0.807	0.814	0.827	0.825	—

Alaska (ca. 1300 km), no evidence of reproductive isolation was apparent between these two northern populations (Table 2b; PALMER, 1984a). All but one F1 hybrid cross yielded viable offspring (Table 2b). In addition, of 28 crosses initiated with offspring from all six hybrid lines between these two distant northern populations, all but one yielded viable F2 offspring: 80-1 (six crosses), 80-2 (eight crosses), 80-3 (four crosses), 80-4 (three crosses, one of which yielded no capsules), 80-11 (one cross), and 80-13 (six crosses). Thus, these hybrids exhibited normal fertility.

Isolation by Distance or Two Discrete Species?

Because of the distance ($\geq$1800 km) between the Californian (Santa Barbara) population and those from the northeastern Pacific (Bamfield and Torch Bay) examined in this study, and because of the low gene flow presumably associated with direct development (GRANT & UTTER, 1988), the reproductive isolation observed between these distant populations could reflect either isolation by distance (WRIGHT, 1943), where all adjacent populations along the coast could interbreed, or the presence of two discrete species. Taken together, however, the concordant patterns of variation in the form of spiral shell sculpture, egg-capsule morphology, and in allozymes all suggest the presence of two discrete species.

Shell sculpture also varied in a manner consistent with two discrete species. Among shells that exhibited spiral sculpture, regularly spaced knobs along the distal margin of the ribs only occurred south of San Francisco Bay (Figure 4). The absence of this form of sculpture north of San Francisco Bay suggested that if two species did exist, the southern one did not extend north of this area. This pattern alone, however, also could have been produced by a genetically based sculpture polymorphism where the allele for "knobby ribs" had not yet crossed the mouth of San Francisco Bay. Evidence for Mendelian inheritance of shell sculpture already exists for Vancouver Island populations of *Nucella emarginata* (PALMER, 1985b).

The allozyme data provide the most convincing evidence for two discrete species (Tables 3, 5, Figure 5). Fixed allelic differences, the presence of novel alleles at moderate frequency in Halfmoon Bay, and the high genetic distance between the Halfmoon Bay and Pillar Pt. populations, which were less than 500 m apart, all suggest that no gene flow was occurring between these two populations. Although no simple relationship exists between genetic distance and taxonomic level, the discovery of a genetic distance of $D = 0.16$ between these adjacent samples was unexpected for conspecific populations. Not only were the four remaining San Francisco area samples virtually identical ($D = 0.00$–0.01; Table 5), but the genetic distance between the Halfmoon Bay and Pillar Pt. populations ($D = 0.16$), which were separated by less than 500 m, was comparable to that observed between Pillar Pt. and Bamfield ($D = 0.18$), which were separated by a distance of more than 1300 km.

Before proceeding further, remember that allozyme differences are probably not directly involved in the speciation process. Although a relationship may exist between degree of genetic differentiation and taxonomic status in some groups of mollusks, a quantitative relationship is not predictable from first principles. Nonetheless, we note that in a survey of over 7000 comparisons of conspecific populations, only 2% of the intraspecific D estimates exceeded 0.10 (THORPE, 1983). A review of published intraspecific and interspecific genetic distances in mollusks supports our interpretation of the separate species-level status of the Halfmoon Bay population (STAUB *et al.*, 1990; WOODRUFF *et al.*, 1988).

Consistent with the allozyme differences, the egg capsules produced by snails from Pillar Pt. were of the "northern" form while those from Halfmoon Bay snails were "southern" in appearance (Figure 2c and e, respectively). Therefore, although the Pillar Pt. snails did not exhibit strong enough spiral sculpture to determine its form, differences in egg-capsule morphology between these two populations also support our interpretation of two discrete species.

Other ecological differences also exist between these two

putative species. Northern populations of *Nucella emarginata* feed almost exclusively upon balanomorph barnacles and mussels, and rarely on limpets (PALMER, 1980, 1988). Southern populations, on the other hand, feed commonly upon the gooseneck barnacle *Pollicipes* and consistently, although in low frequency, upon limpets (WEST, 1986). In addition, individuals in northern populations do not exhibit any evidence of "majoring" (HEINRICH, 1979) on particular prey types (PALMER, 1984b), while those in southern populations do (WEST, 1986).

Shell Form and Cryptic Species

The discovery of two morphologically very similar species within the current taxon *Nucella emarginata* highlights the difficulty of recognizing species based upon differences in shell form. Cryptic species have recently been identified by allozyme differences in several prosobranch genera including *Brotia* (KLINHOM, 1989), *Collisella* (MURPHY, 1978), *Crepidula* (HOAGLAND, 1984), *Goniobasis* (CHAMBERS, 1980), *Littorina* (MASTRO *et al.*, 1982; BOULDING, 1990), *Neotricula* (STAUB *et al.*, 1990), *Oncomelania* (WOODRUFF *et al.*, 1988), and *Robertsiella* (YONG *et al.*, 1985). Given the extent to which shells may vary within species, particularly in thaidine gastropods (CROTHERS, 1984; APPLETON & PALMER, 1988, and references therein), more cryptic species seem likely to be discovered.

Other Levels of Variation

Although chromosome differences are often associated with speciation (WHITE, 1978), a preliminary study of chromosome variation among northeastern Pacific *Nucella* revealed that all four species recognized at the time (*canaliculata, emarginata, lamellosa,* and *lima*) had the same haploid chromosome number ($n = 35$; AHMED & SPARKS, 1970). The constancy within and among these species suggests that the two cryptic species identified here will also lack differences in chromosome number.

This lack of chromosome variation in northeastern Pacific species is surprising in view of the striking polymorphism observed in the north Atlantic *Nucella lapillus*. In populations of *N. lapillus* from northern France, the haploid chromosome number varies more or less continuously from $n = 18$ to $n = 13$ over a wave-exposure gradient (STAIGER, 1954). In a much more detailed study, BANTOCK & COCKAYNE (1975) found this polymorphism to be limited to shores of southern England. More northern populations from the Bristol Channel and from the Straits of Dover were monomorphic for a haploid chromosome number of $n = 13$ (BANTOCK & COCKAYNE, 1975), as were both protected- and exposed-shore populations from the coast of Norway (HOXMARK, 1970). The larger scale correlation of chromosome number with latitude suggests that perhaps these chromosome forms reflect northern and

southern races of *lapillus* that diverged in isolation and have since come back into contact. The common occurrence of intermediates in areas where both forms coexist (BANTOCK & COCKAYNE, 1975; STAIGER, 1954), however, indicates that hybrids are perfectly viable and that these chromosome differences are probably not associated with cryptic species.

Taxonomic Status of the New Species

Which of the two cryptic species identified above will retain the name *emarginata*? This question is not as straightforward as it might seem. In his second description, published in French, DESHAYES (1841) illustrated a shell whose form of spiral sculpture was ambiguous (spiral ribs were not clearly uniform or knobby). To exacerbate the situation, he cited the type locality as New Zealand! DALL (1915), without explaining the basis of his decision, reassigned the type locality to San Miguel Id., in the channel islands of California near Santa Barbara (see Figure 4). This new type locality would lie within the range of the putative southern taxon identified here.

To complicate matters further, generic relations within the Thaidinae are in a state of flux (KOOL, 1987). *Nucella* is the genus to which the northeast Pacific species previously called *Thais* are now referred (*e.g.,* KOZLOFF, 1987; MORRIS *et al.,* 1980; SMITH & CARLTON, 1975), and *Nucella* may in fact not be a true thaidine (KOOL, 1988). The evidence upon which this generic reassignment has been made is discussed at length in KOOL (1989).

Several synonyms and varietal names are available for *Nucella emarginata* (cited in DALL, 1915), including: *anomala* (Middendorff, 1849), *ostrina* (Gould 1852), *saxicola* (Carpenter, 1864), and *projecta* (Dall, 1915). *Nucella fuscata* [*Purpura*] (Forbes 1850; as cited in VANATTA, 1910) may also be eligible. We suggest that until a description and synonymy is completed, studies of "*Nucella emarginata*" should include a collection of egg capsules, and shells with well developed sculpture. Temporarily, at least, the species could be called *Nucella emarginata* (northern) and *Nucella emarginata* (southern).

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Survey for Functional Kleptoplasty Among West Atlantic Ascoglossa (=Sacoglossa) (Mollusca: Opisthobranchia)

by

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Abstract. Eighteen species of Florida and New England Ascoglossa were examined for chloroplast retention and photosynthetic function, to more precisely delimit the occurrence and determine the levels of kleptoplasty (=chloroplast symbiosis). Previously unexamined genera with functional plastids include *Mourgona, Caliphylla, Bosellia,* and *Placida.* Short-lived function was also detected in *Alderia. Bosellia mimetica* exhibited high levels of carbon fixation, and is probably equivalent to the best-developed examples of kleptoplasty. Three examples of elysiids without functional plastids were found: *Elysia serca* and *E. catulus,* feeding upon seagrasses, and *E. evelinae,* feeding upon diatoms. Six levels of kleptoplasty, in terms of plastid retention and function, are recognized in this paper.

Some shelled Ascoglossa maintain structurally intact plastids for one to several days, but without detectable photosynthetic function. This capability appears to be precursory to retention of functional kleptoplastids and may initially have simply enhanced cryptic coloration. Retention of functional kleptoplastids is a plesiomorphic character among both elysioid and stiligeroid lines, and loss of function among advanced taxa is due partially to adaptive radiation to unsuitable plastid sources. Determination of whether functional kleptoplasty evolved convergently in elysioid and stiligeroid lines, or within a shared ancestor, cannot presently be answered.

INTRODUCTION

The retention of chloroplasts by ascoglossan mollusks was first noted by BRÜEL (1904) in *Caliphylla mediterranea* Costa, 1867, and was subsequently rediscovered by KAWAGUTI & YAMASU (1965) in *Elysia atroviridis* Baba, 1955. This phenomenon has been described as "chloroplast symbiosis." However, various authors have sought a more appropriate term (TAYLOR, 1968; BLACKBOURN *et al.,* 1973; TRENCH, 1980), and we support use of the term "kleptoplasty" (GILYAROV, 1983; WAUGH & CLARK, 1986).

Views on the extent of chloroplast retention have varied; GREENE (1970a) suggested a broad occurrence of kleptoplasty among the order, while MUSCATINE & GREENE (1973) and TRENCH (1975) indicated a much restricted occurrence, principally to Elysiidae feeding on Siphonales. However, exceptions to this were known. *Hermaea bifida*

(Montagu, 1816), feeding on the rhodophyte *Griffithsia* (TAYLOR, 1971; KREMER & SCHMITZ, 1976) retained functional plastids, as did the stiligerid *Limapontia depressa* Alder & Hancock, 1862 (interpreted by TRENCH [1975] as an elysiid), feeding upon *Vaucheria* (HINDE & SMITH, 1974). CLARK & BUSACCA (1978) summarized evidence for a broader occurrence of kleptoplasty. CLARK *et al.* (1981) found that *Costasiella ocellifera* (Simroth, 1895) retained highly functional plastids for a period equivalent to that of *Elysia (Tridachia) crispata* (Mörch, 1863), previously recognized as the best example of functional plastid retention (TRENCH, 1975).

Determining the occurrence of kleptoplasty within the order should provide important information on evolution of the Ascoglossa. Of approximately 200 described species, only about 10% have been examined for kleptoplasty. Several families (Ascobullidae, Volvatellidae, Caliphyllidae, Boselliidae, and Gascoignellidae) have not been studied. In this paper, we present results of a systematic examination of 18 west Atlantic species representing 5 additional families, 14 genera, and 14 plant species.

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Table 1

Sources of experimental material.

Ascoglossan species	Locality	Diet/substrate
Conchoidea		
Ascobulla ulla Marcus, 1970	Fort Pierce, FL	*Caulerpa racemosa* (Forsskål) J. Agardh
Lobiger souverbiei Fischer, 1856	Sebastian Inlet, FL	*Caulerpa racemosa*
Oxynoe azuropunctata Jensen, 1980	Key Largo, FL	*Caulerpa paspaloides* (Bory) Greville
Berthelinia caribbea Edmunds, 1963	Deepwater Cay, Bahamas	*Caulerpa verticillata* J. Agardh
Stiligeroidea		
Caliphylla mediterranea Costa, 1867	Fort Pierce, FL	*Bryopsis plumosa* (Hudson) C. Agardh
Mourgona germaineae Marcus & Marcus, 1969	Geiger Key, FL	*Cymopolia barbata* (Linnaeus) Lamouroux
Cyerce antillensis Engel, 1927	Fort Pierce, FL	*Cladophora prolifera* (Roth) Kützing
Aplysiopsis zebra Clark, 1982	Key Largo, FL	*Penicillus dumetosus* (Lamouroux) Blainville
Hermaea cruciata Gould, 1870	Key Largo, FL	*Griffithsia* sp.
Placida dendritica (Alder & Hancock, 1843)	Noank, CT	*Codium fragile* (Suringar) Hariot
Placida kingstoni Thompson, 1977	Fort Pierce, FL	*Bryopsis plumosa*
Ercolania fuscata (Gould, 1870)	Sebastian Inlet, FL	*Cladophora gracilis* (Griffiths *ex* Hárvey) Kützing
Ercolania coerulea Trinchese, 1893	Long Key, FL	*Dictyosphaeria cavernosa* (Forsskål) Børgesen
Alderia modesta (Lovén, 1844)	Gloucester Pt., VA	*Vaucheria* sp.
Elysioidea		
Elysia serca Marcus, 1955	Banana River, FL	*Halophila engelmannii* Ascherson in Neumayer
Elysia catulus (Gould, 1870)	Noank, CT	*Zostera marina* (Linnaeus)
Elysia evelinae Marcus, 1957	Key Largo, FL	*Biddulphia* sp.
Bosellia mimetica Trinchese, 1891	Fort Pierce, FL	*Halimeda tuna* (Ellis & Solander) Lamouroux

MATERIALS AND METHODS

Collection sites and food species for animals used in this study are shown in Table 1. Animals were collected from 1979 to 1980 at sites in Bermuda, the Bahamas, Florida, Connecticut, and Maryland. A voucher collection for species used in this study was previously deposited with the National Museum of Natural History (JENSEN, 1980). Specimens of *Oxynoe azuropunctata* and *Berthelinia caribbea* were laboratory-cultured from stocks collected at the listed sites. Animals were kept in the laboratory in 40-L aquaria with natural seawater and excess food until used for experiments. Aquarium temperature was approximately 25°C, and the aquaria were illuminated by a bank of fluorescent bulbs at an intensity of approximately 110 $\mu Ei \cdot m^{-2} \cdot sec^{-1}$ and a photoperiod of 18 hr light : 6 hr dark.

Ultraviolet epifluorescence was used to determine presence and persistence of intact chlorophylls in freshly fed slugs and in animals starved for various intervals. Bright red fluorescence, confined to plastids in digestive diverticula, suggested the possibility of photosynthetic activity, and these species were further examined by radiocarbon incubation.

Experimental animals were incubated individually for 1 hr in 2- or 4-mL vials containing membrane-filtered seawater (MFSW) and labelled $NaH^{14}CO_3$ at an activity of 2 $\mu Ci/mL$. Most animals were incubated at a light intensity of 350 $\mu Ei \cdot m^{-2} \cdot sec^{-1}$ and a temperature of 25°C after several days of laboratory maintenance. However,

some species in which we suspected plastid activity might be short-lived or subject to effects such as toxin inhibition were incubated *in situ* immediately after collection by placing the incubation apparatus at the site of collection. Thus, *Alderia modesta* was tested *in situ* at 1650 $\mu Ei \cdot m^{-2} \cdot sec^{-1}$ and 24°C. *Placida dendritica* and *Elysia catulus* were incubated *in situ* at 400 and 650 $\mu Ei \cdot m^{-2} \cdot sec^{-1}$, respectively, and 16°C. Dark controls were wrapped in aluminum foil and run simultaneously.

Following incubation, animals were quickly rinsed in three changes of MFSW to remove residual isotope and homogenized in 0°C methanol; chlorophyll was extracted by phase separation in diethyl ether and distilled water. Chlorophyll content was determined spectrophotometrically after the following equation (STRAIN & SVEC, 1966):

$$\mu g \ chl/mL = 7.12(Ab_{660}) + 16.8(Ab_{642.5}),$$

where Ab is the absorption at the indicated wavelength (nm).

The alcohol/aqueous (A/A) phase was centrifuged at 15,000 rpm for 20 min. A 100-μL aliquot of the supernatant was mixed with 10 mL Aquasol and counted in a liquid scintillation counter (LSC). The volume of the A/A phase was measured. The centrifuged pellet was solubilized in 1 mL tissue solubilizer and neutralized with acetic acid, and a 100-μL aliquot was used for liquid scintillation counting. Total CPM was corrected for counting efficiency, quenching, and background, and counts were calculated as $DPM \cdot \mu g$ chlorophyll$^{-1} \cdot hr^{-1}$ (A/A and tissue-solubil-

Table 2

Summary of carbon fixation experiments in west Atlantic Ascoglossa. Chlorophyll retention: 0, no chlorophyll recoverable from freshly fed animals; 1, less than 12 hr; 2, 12 hr to 3 days; 3, 3 days to 1 wk; 4, longer than 1 wk. D.P.M. = disintegrations per minute; d.f. = degrees of freedom; t = calculated value of Student's "t"; P = significance level; L:D = ratio of light to dark fixation.

Ascoglossan species	Light fixation (D.P.M.)	Dark fixation (D.P.M.)	Chlor. reten. times	d.f.	t	P	L:D
Conchoidea							
Ascobulla ulla	(no pigment)		0	—	—	—	—
Lobiger souverbiei	6090 ± 4500	2810 ± 3270	2	6	1.18	n.s.	2.16
Oxynoe azuropunctata	4050 ± 3310	3150 ± 1710	2	20	0.78	n.s.	1.30
Berthelinia caribbea	1660 ± 1520	1150 ± 700	2	19	0.97	n.s.	1.45
Stiligeroidea							
Caliphylla mediterranea	1100 ± 880	107 ± 58.5	3	5	2.55	<0.05	2.88
Mourgona germaineae	5070 ± 2090	3170 ± 1260	3	13	2.17	<0.05	1.59
Cyerce antillensis	670 ± 82	543	1	1	n.a.	—	1.23
Aplysiopsis zebra	1860 ± 1020	1420 ± 362	1	10	0.99	n.s.	1.31
Hermaea cruciata	2550 ± 1280	2040 ± 939	2	6	1.01	n.s.	1.25
Placida dendritica	296 ± 115	290 ± 163	2	9	0.07	n.s.	1.02
Placida kingstoni	1230 ± 254	769 ± 261	2	12	3.31	<0.01	1.60
Ercolania fuscata	4820 ± 1780	6080 ± 3780	0	9	−0.73	n.s.	0.79
Ercolania coerulea†	618 ± 493	3493 ± 5193	1	11	1.60	n.s.	0.18
Ercolania coerulea‡	1898 ± 594	2133 ± 9.11	1	11	0.57	n.s.	0.89
Alderia modesta	15,800 ± 8930	5490 ± 5160	1	8	2.35	<0.05	2.88
Elysioidea							
Elysia serca‡	1150 ± 1040	959 ± 708	1	10	0.38	n.s.	1.20
Elysia catulus‡	1110 ± 491	1750 ± 980	1	14	−1.66	n.s.	0.63
Elysia evelinae	(pigment traces)		0/1	—	—	—	—
Bosellia mimetica	20,500 ± 4880	702 ± 146	4	3	5.44	<0.02	29.2

† Chlorophyll-specific rate.

‡ Rate per animal (non-chlorophyll-specific).

izer counts were summed). The ether phase contained negligible activity.

Preliminary examination of *Ascobulla ulla* and *Elysia evelinae* showed that chlorophyll was absent in freshly fed animals, so animals were not assayed for carbon fixation. Values for *Elysia catulus* and *Elysia serca* were based on fixation per animal, because most chlorophyll values were so low that meaningful pigment-specific data could not be calculated. Both rates were calculated for *Ercolania coerulea* because chlorophyll values for dark-incubated animals were significantly lower than those for light-incubated animals (t = 2.73, d.f. = 11, P < 0.02).

RESULTS

Carbon fixation data are summarized in Table 2. No net fixation occurred in the shelled species examined, though chlorophylls were retained up to several days in these species (see also CLARK & BUSACCA, 1978). *Ascobulla ulla* and *Elysia evelinae* apparently degrade chlorophylls immediately upon ingestion, and hence were not examined for radiocarbon fixation.

Among the stiligeroids, four species (*Caliphylla mediterranea*, *Mourgona germaineae*, *Placida kingstoni*, and *Alderia modesta*) fixed significantly more carbon in light than in darkness. Of these species, *C. mediterranea* has the highest fixation (verifying BRÜEL's 1904 report), with photosynthetic activity probably lasting as long as a week. Unfortunately, a shortage of experimental material prevented more precise determination of the duration of photosynthetic activity. *Mourgona germaineae* appears to have similar functional ability, but this species is difficult to study because autotoxicity of stored cymopols (JENSEN, 1984) requires large incubation volumes and consequently large quantities of isotope. Fixation ability of *A. modesta* is short-lived, as chlorophylls are retained in diverticula less than 12 hr. This may explain prior reports of non-functionality (HINDE & SMITH, 1974; GRAVES *et al.*, 1979). The remaining stiligeroid species did not exhibit significantly higher fixation in light than in dark.

Among the elysioid species, neither *Elysia catulus* nor *E. serca* possessed functional plastids, and chlorophyll retention was brief. Although traces of chlorophyll occur in freshly fed *E. evelinae*, plastids fluoresce weakly, and the

presence of diffuse plastid margins immediately after feeding indicates rapid digestion. Therefore, we assume this species has non-functional retention. *Bosellia mimetica*, however, fixes large amounts of carbon (L:D ratio of 30), and based on chlorophyll retention, probably retains highly functional plastids for periods equivalent to those of other pronounced examples of kleptoplasty such as *Elysia* (*Tridachia*) *crispata* (TRENCH & OHLHORST, 1976) and *Costasiella ocellifera* (CLARK *et al.*, 1981).

DISCUSSION

TRENCH (1975) proposed a restrictive criterion for recognition of kleptoplasty: high light fixation rates for more than a week. We feel that the exclusion of less pronounced activity discourages scrutiny of the coevolution of ascoglossans and their algal foods. Based on present results and prior studies, we recognize a gradient between the extremes of non-retention of plastids and long-term retention, and propose the following six stepped levels of kleptoplasty and their criteria:

Level 1. Non-retention: Animal feeds on algal food that has potential as a plastid donor, but plastids are digested prior to, or immediately after, phagocytosis. The digestive diverticula lack algal pigments. Only *Ascobulla*, and perhaps the burrowing species of *Volvatella* (*e.g.*, *V. laguncula* Thompson, 1979) seem to have non-retention.

Level 2. Short-term, non-functional retention: Animal is pigmented when collected and retains plastids in gut diverticula for at least 2 hr of starvation, but no photosynthate is detectable by isotope tracer techniques. Retention time may vary with illumination. *Elysia catulus, Elysia evelinae,* and *Ercolania coerulea* are examples. The rapid loss of chlorophyll in darkness by *Elysia catulus* suggests that illuminated plastids may somehow inhibit digestion of plastids despite absence of detectable carbon fixation. *Polybranchia viridis* Pease, 1869, rapidly degrades chlorophylls and is pronouncedly photophobic (Clark, personal observation), and thus would also fit this category.

Level 3. Medium-term, non-functional retention: Structurally intact plastids occur at least 24 hr (including one interval of darkness) after ingestion, but no photosynthetic activity can be demonstrated. This category includes most advanced conchoid Ascoglossa (Lobigeridae, Oxynoidae, and Juliidae), and epifaunal *Volvatella* (STIRTS, 1980; CLARK, 1982a; and present study).

Level 4. Short-term functional retention: Animal exhibits photosynthesis in field environment, but plastids are rapidly digested and function ceases less than one day after removal from field environment. *Alderia modesta* meets this criterion, and some others, such as *Hermaea cruciata,* may fit into this category when more rigorously examined.

Level 5. Medium-term functional retention: Photosynthesis persists for more than 24 hr, including a period of darkness, but photosynthesis ceases or is greatly reduced within a week of starvation, *Hermaea bifida* appears to fit this level (TAYLOR, 1971).

Level 6. Long-term functional retention: Photosynthesis persists for more than a week in starved animals. *Elysia* (*Tridachia*) *crispata, Bosellia mimetica, Limapontia depressa,* and *Costasiella ocellifera* fall in this category.

In the discussion of phylogenetic patterns below, we have followed a consensus of familial relationships based on recent works of several authors. CLARK & BUSACCA (1978) constructed a phylogeny based upon papers by BOETTGER (1963), BABA (1966), and KAY (1968), and showed that an adaptive radiation in ascoglossan diets has closely paralleled anatomical radiation. In this pattern, primitive ascoglossans feed upon *Caulerpa* (as shown by KAY, 1968), and progressively more advanced taxa feed on other Siphonales, Siphonocladales, Cladophorales, and then a variety of other foods. Following GASCOIGNE's (1985) revision, we have reduced the number of Conchoidea families to three. Relationships of stiligeroid families were derived by GASCOIGNE (1976) from reproductive anatomy, and by CLARK (1982b) based on other anatomical characteristics. The dietary radiation has been confirmed for *Elysia* species with genetic analysis using starch gel electrophoresis (NUTTALL, 1987), with *Caulerpa* as the food of primitive species and other algae as foods of advanced species. Additional support for the phylogeny was provided by CLARK & DEFREESE (1987) based on habitat characteristics.

When the six levels of kleptoplasty are considered together with familial relationships, a pattern begins to emerge (Figure 1). The first indication of kleptoplasty—the retention of non-functional plastids—occurs in shelled ascoglossans, whereas functional plastids appear in most elysiacean (parapodium-bearing) families and irregularly among species in the stiligeroid (cerata-bearing) families. Functional kleptoplasty appears to be a primitive character among elysiids, with secondary loss among species that have adopted unusual diets (*Elysia serca, E. catulus,* and *E. evelinae*). Among the stiligeroid families, highly functional plastids appear among more primitive families (Caliphyllidae and Costasiellidae) feeding upon Siphonales and Dasycladales. With increasing ecological and dietary specialization, forms of kleptoplasty appear to progressively weaken. Thus, in the Hermaeidae, *Hermaea bifida* shows well-developed functional kleptoplasty (level 5), while *H. cruciata* has level 3 retention, and *Aplysiopsis smithi* (Marcus, 1961) (GREENE, 1970b) and *A. zebra* have non-functional retention (level 2). Among the Stiligeridae, most species have non-functional retention (levels 2 and 3), though functionality may appear in species that feed on primitive foods, such as *Placida kingstoni* on *Bryopsis*. However, some other species, utilizing Siphonocladales (*Ercolania coerulea* on *Dictyosphaerium*), do not maintain functional plastids. This suggests that there are taxon-specific factors that need to be identified. Possibly the benefits of kleptoplasty are incongruent with the opportunistic growth strategies characteristic of most stiligerids and hermaeids (CLARK, 1975; CLARK & DEFREESE, 1987), and the physiological demands of functional kleptoplastids (CLARK *et al.*, 1979; HINDE & SMITH, 1975) may interfere
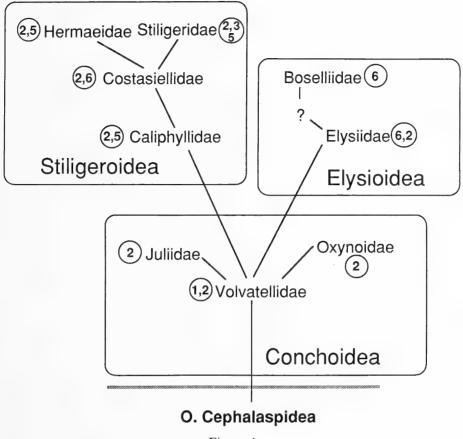
Figure 1

Distribution of the six levels of kleptoplasty in relation to provisional phylogeny of the Ascoglossa. The phylogeny is based on anatomical, dietary, and genetic analyses by CLARK & BUSACCA (1978), GASCOIGNE (1985), and NUTTALL (1987).

with rapid growth. As previously noted (MUSCATINE & GREENE, 1973), the Cladophorales are structurally unsuitable for kleptoplasty, which explains the non-functionality in most Stiligeridae and in *Aplysiopsis*, which feed primarily on this group.

The most primitive ascoglossan, *Ascobulla*, does not retain plastids at all. However, these mollusks normally live below the sediment surface, without light, where kleptoplastids would be useless. During brief periods in which *Ascobulla* crawls on the sediment surface (DEFREESE, 1987), retention of pigmented plastids might also increase predation. The remaining conchoidean species are all epialgal, and all exhibit level 2 or 3 (short- or medium-term, nonfunctional) retention. This relationship probably functions in nutritional homochromy, as intact plastids provide cryptic coloration virtually identical to that of the host alga. Molluscan intracellular digestion and the resistant plastids of siphonalean algae (GILES & SARAFIS, 1972) are preadaptive characteristics that probably favored early appearance of this level in epifaunal species. This level of kleptoplasty should be considered a plesiomorphic trait,

preadaptive to development of functionality among shell-less clades. On an anatomical level, the division of plastid diverticular cells into two types, one of which retains plastids, occurs among volvatellids and all higher families (STIRTS, 1980).

It is unclear why conchoidean species did not evolve photosynthetically functional kleptoplasty. However, the presence of a shell seems likely involved in this limitation. One possibility is that calcium metabolism and carbonate equilibria are somehow involved. For example, metabolically generated CO_2 is used in molluscan shell deposition (WILBUR, 1964), and metabolism keyed toward shell deposition may limit photosynthetic rate by reducing carbonate availability. Cladohepaty (branching of the digestive gland) seems a necessary feature for photosynthetic function, because this feature occurs in all species with functional plastids, but is not sufficient, because partial cladohepaty occurs in both *Volvatella* and the Juliidae (CLARK & BUSACCA, 1978; CLARK, 1982a). The Oxynoidae (including *Lobiger*) are all holohepatic. Cladohepaty is plesiomorphic to both the stiligeroid and elysioid lines

and may also be preadaptive to photosynthetically functional kleptoplasty.

Precise relationships between Volvatellidae, primitive Elysioidea (parapodium-bearing taxa), and primitive Stiligeroidea are presently unclear. However, functional plastid retention appeared early in both the elysioid and stiligeroid lines, occurring in caulerpivorous elysiids and in caliphyllids feeding on siphonocladalean algae. Both these dietary patterns are apparently plesiomorphic in their respective clades (CLARK & BUSACCA, 1978; CLARK & DEFREESE, 1987; NUTTALL, 1987). However, this does not solve the problem of the origin of functional kleptoplasty, for we do not know whether the Stiligeroidea and Elysioidea had a common shell-less ancestor, in which function first appeared, or whether these clades were derived separately from shelled, cladohepatic forms (probably volvatelloid), with convergent evolution of functional kleptoplasty in each line. Because the two major preadaptive changes, cladohepaty and supportive diverticular cells, appear precursorily in two families of Conchoidea, the change between non-functional and functional kleptoplasty may have involved a very small genetic change, such as partial suppression of immune recognition, or translocation of a few genes from plastid/plant to animal genome. CLARK & DEFREESE (1987) suggested that functional plastid retention may have increased fitness among early shell-less forms by compensating for difficulty in feeding on calcified Siphonales.

Kleptoplastic abilities of two families remain uninvestigated: Platyhedylidae and Gascoignellidae. These highly modified shell-less forms have uncertain relationships with other families, and knowledge of their diets and kleptoplastid retention capabilities might clarify these. *Gascoignella aprica* Jensen, 1985, the only known gascoignellid, has dark green diverticula, but these are shielded by melanic pigment, a character usually associated with non-functional plastids, as in the black form of *Limapontia depressa* (HINDE & SMITH, 1974), and in *Ercolania fuscata* and *Elysia catulus* (present study).

Considered at the generic level, and excepting the primitive shelled species, GREENE's (1970b) perception of widespread distribution of functional kleptoplastids is probably the most appropriate view. The ability to maintain functional kleptoplastids occurs in most shell-less genera (though it may be absent in some species of a genus and among ecotypes). Its absence may be related to inappropriate plastid structure, and such other factors as light, temperature (STIRTS & CLARK, 1980), and life-history strategies (WAUGH & CLARK, 1986; CLARK & DEFREESE, 1987). The widespread occurrence of functional kleptoplasty among Elysiidae should be considered primarily the result of retention of an evolutionarily conservative diet of siphonalean algae, and not an evolutionarily advanced condition.

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Range Limits and Dispersal of Mollusks in the Aleutian Islands, Alaska

by

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Abstract. The Aleutian-Commander arc of islands linking Alaska and Kamchatka provides a dispersal corridor for North Pacific species. A biogeographical analysis of 109 shallow-water shell-bearing molluscan species collected during two expeditions to the Aleutian Islands has yielded several new westward range extensions of eastern Pacific species and some eastward extensions of western Pacific species. These include *Lottia digitalis* (Rathke, 1833), west to Kiska; *Opalia borealis* (Keep, 1881), west to Adak; *Nucella lamellosa* (Gmelin, 1791), west to Nizki; *Plicifusus stejnegeri* (Dall, 1884), east to Nizki; *Volutopsius pallidus* Tiba, 1973, east to Adak; and *Amphissa columbiana* Dall, 1916, west to Chuginadak. Aleutian and Bering Sea records of *Nucella emarginata* (Deshayes, 1839) are erroneous; this species (in the broad sense) reaches its northern limit somewhere between Yakutat, southeastern Alaska, and Kodiak Island in the northern Gulf of Alaska.

Contrary to the pattern in warm-water faunas, in which pelagic larval stages are linked to broad geographical ranges, Aleutian species with planktonically dispersing larval stages are not more likely to have wider east–west distributions (that is, to be distributed in a continuum across the North Pacific) than are species with nonplanktonic larvae.

INTRODUCTION

The cool-temperate North Pacific Ocean supports an exceptionally rich biota that, despite a few episodes of extinction and of invasion from other faunas, has remained a distinct entity since at least late Eocene time. The two predominant biogeographical components are an eastern Pacific element, evolving on the American side, and a western Pacific element, evolving in Asia. During the late Paleogene and Neogene, these biotic components exchanged species through eastward and westward dispersal, with the result that many taxa came to be distributed on both sides of the North Pacific (KILMER, 1978; KAFANOV, 1984). Links between the eastern and western North Pacific seem to have been especially strong during warm intervals of the middle and late Miocene (MARINCOVICH & KASE, 1986; MARINCOVICH, 1988) and, although many of these links have subsequently been severed as indicated by the existence of species pairs of eastern and western Pacific species in lineages with formerly continuous ranges across the North Pacific (KEEN, 1941; VERMEIJ, 1989), many species maintain a continuous range from east to west in the North Pacific today.

This link is most likely to be maintained along two corridors, the region of Bering Strait near the Arctic Circle, and the Aleutian-Commander chain of islands between the Alaska Peninsula and Kamchatka. For both corridors, dispersal across a water barrier is prerequisite for maintain-
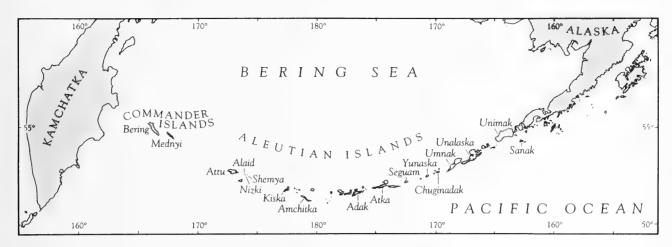
Figure 1

Map of Aleutian-Commander arc.

ing continuity of range. Such dispersal could occur by a planktonic larval stage or by rafting or floating at any stage in the life cycle. In some cases, the benthic adults may live in water deep enough that inter-island barriers do not inhibit dispersal.

A collecting expedition by Vermeij and Palmer aboard the R/V *Alpha Helix* to 11 of the Aleutian Islands during the summer of 1987 provided an opportunity to study range limits in relation to larval dispersal mode among common shallow-water shell-bearing mollusks. Several new eastern and western geographical range limits were established, which forced us to think about why some species fail to extend continuously across the North Pacific despite a pelagic dispersal phase. This paper is an outgrowth of our observations, together with an analysis of Lindberg's collections made at Attu in 1979.

MATERIALS AND METHODS

Mollusks were collected by hand in the intertidal zone and from rocky bottoms to a depth of 10 m at the following islands, listed from west to east (Figure 1): Near Islands (Attu, Nizki, Shemya), Rat Islands (Kiska and Amchitka), Andreanof Islands (Adak), and Fox Islands (Seguam, Yunaska, Chuginadak, Umnak, and Unalaska). The subtidal specimens were collected by D. O. Duggins, J. A. Estes, D. Irons, K. A. Miller, and J. Watson during field studies of sea otters and kelps (see DUGGINS *et al.*, 1989). Intertidal collections were made by Vermeij and Palmer. In 1979, Lindberg made intertidal and subtidal collections at Attu. His material, together with a few specimens of the 1987 expedition, is housed at the Los Angeles County Museum of Natural History; the rest is in the Vermeij collection.

Gastropods and pelecypods were critically examined and identified by Vermeij, Lindberg, Palmer, J. H. McLean, and R. Baxter. D. Ernisse kindly identified most polyplacophorans. Geographical range limits and distributions

were compiled from a critical survey of the literature (GOLIKOV & GULBIN, 1977; GOLIKOV & KUSSAKIN, 1978; KUSSAKIN & coworkers, 1978; LINDBERG, 1981, 1982, 1988; FOSTER, 1981; SCARLATO, 1981; BAXTER & McLEAN, 1984; BAXTER, 1987; REID, 1989) and through inspection of the collections at the Los Angeles County Museum of Natural History and the U.S. National Museum of Natural History. Probable mode of larval dispersal was determined mainly from STRATHMANN (1987) and BERNARD (1979) and references therein.

RESULTS

A list of the 109 species of mollusks in our collections is given in Table 1, together with distributions in the Aleutian-Commander arc and inferred mode of larval dispersal. This number represents a minority of the molluscan species known from the Aleutians, but our species are biogeographically more or less typical of the fauna as a whole. Our critical review of BAXTER's (1987) compilation shows that 222 of the 396 shell-bearing molluscan species reported by him and by us from the Aleutians (56%) have ranges extending across the North Pacific from the mainland coast of Alaska to the mainland coast of Asia: 157 species (39%) are eastern Pacific species with their western range limits in the Aleutians, and 17 species (4.3%) are Asian species with their eastern limits in the Aleutians. The comparable percentages for our species are 71% (amphi-Pacific), 23% (eastern Pacific), and 5.5% (western Pacific). Our calculations from Baxter's lists must be treated with caution in view of many taxonomic and distributional uncertainties, especially for the deep-water species that Baxter included but that are unrepresented in our material.

Several of the species listed in Table 1 require comment. They are discussed in the following paragraphs.

Puncturella longifissa Dall, 1914. This northwestern Pacific species of keyhole limpet was previously recorded as

Table 1

Shallow-water marine shell-bearing mollusks collected in the Aleutian Islands. Key: +, ranging throughout Aleutian Islands; B, nonplanktonic larva; P, planktonic larva.

Species	Aleutian range	Larval type
Gastropoda		
Anatoma obtusata (Golikov & Gulbin, 1978)	+	B
Puncturella (*P.*) *longifissa* Dall, 1914	Adak west	
P. (*Cranopsis*) *major* Dall, 1891	Kiska east	
Erginus (*E.*) *puniceus* Lindberg, 1988	Attu west	B
E. (*E.*) *apicina* (Dall, 1879)	+	B
E. (*Problacmaea*) *moskalevi* (Golikov & Kussakin, 1972)	Unalaska west	B
E. (*P.*) *sybaritica* (Dall, 1871)	+	B
Lottia borealis (Lindberg, 1982)	+	P
L. digitalis (Rathke, 1833)	Kiska east	P
L. ochracea (Dall, 1871)	+	P
L. painei Lindberg, 1990	Attu east	P
L. pelta (Rathke, 1833)	+	P
Rhodopetala rosea Dall, 1872	+	B
Tectura scutum (Rathke, 1833)	+	P
T. testudinalis (Müller, 1776)	+	P
Acmaea mitra Rathke, 1833	Umnak east	P
Cryptobranchia concentrica Middendorff, 1847	+	P
Margarites (*M.*) *albolineatus* Smith, 1889	+	B
M. (*M.*) *beringensis* Smith, 1899	+	B
M. (*M.*) *helicinus* (Phipps, 1774)	+	B
M. (*Valvatella*) *pupillus* (Gould, 1841)	Umnak east	P
M. (*V.*) *vorticifer* Dall, 1873	+	B
Homalopoma lacunatum Carpenter, 1864	Attu east	
Moelleria costulata (Möller, 1842)	Attu east	
Spiromoelleria quadrae (Dall, 1897)	+	
Lacuna (*Epheria*) *porrecta* Carpenter, 1864	+	P
L. (*E.*) *vincta* (Montagu, 1803)	+	P
Littorina (*Neritrema*) *aleutica* Dall, 1872	+	B
L. (*N.*) *subrotundata* Carpenter, 1864	+	B
L. (*N.*) *sitkana* Philippi, 1846	+	B
Onoba bakeri (Bartsch, 1910)	Attu east	B
O. dinora (Bartsch, 1917)	Attu east	B
O. cerinella (Dall, 1886)	+	B
O. kyskensis (Bartsch, 1912)	+	B
Boreocingula katherinae (Bartsch, 1912)	+	
Barleeia subtenuis Carpenter, 1864	Attu east	B
Cerithiopsis stejnegeri Dall, 1884	+	
Opalia borealis (Keep, 1881)	Adak east	
Melanella columbiana (Bartsch, 1917)	Attu east	
M. randolphi (Vanatta, 1899)	+	
Crepidula grandis Middendorff, 1849	+	P
Trichotropis (*Ariadnaria*) *insignis* Middendorff, 1849	+	
T. (*Turritropis*) *cancellata* Hinds, 1843	+	
Cryptonatica clausa (Broderip & Sowerby, 1829)	+	B
Velutina conica Dall, 1887	+	P
V. prolongata Carpenter, 1864	Attu east	P
V. velutina (Müller, 1776)	+	P
Fusitriton oregonensis (Redfield, 1846)	+	P
Boreotrophon truncatus (Ström, 1788)	+	B
Nucella canaliculata (Duclos, 1832)	Attu east	B
N. lamellosa (Gmelin, 1791)	Nizki east	B
N. lima (Gmelin, 1791)	+	B
Buccinum baeri Middendorff, 1848	+	B
B. glaciale Linnaeus, 1761	+	B
B. picturatum Dall, 1877	+	B
Volutharpa ampullacea (Middendorff, 1847)	+	B
Colus periscelidus (Dall, 1891)	Sanak west	B

Table 1

Continued.

Species	Aleutian range	Larval type
Plicifusus stejnegeri (Dall, 1884)	Nizki west	B
Volutopsius pallidus Tiba, 1973	Adak west	B
Amphissa columbiana Dall, 1916	Chuginadak east	B
Astyris amiantis Dall, 1919	+	B
A. rosacea (Gould, 1840)	+	B
Oenopota harpularia (Couthouy, 1839)	+	
Evalea amchitkana (Dall & Bartsch, 1909)	+	
Philine polaris Aurivillius, 1887	+	
Liriola thersites Carpenter, 1864	+	B
Pelecypoda		
Crenella leana (Dall, 1897)	+	
Musculus discors (Linnaeus, 1767)	+	B
Mytilus (Pacifimytilus) californianus Conrad, 1837	Amchitka east	P
M. trossulus Gould, 1850	+	P
Modiolus modiolus (Linnaeus, 1758)	+	P
Vilasina vernicosa (Middendorff, 1849)	+	
Chlamy sp.		
Pododesmus macrochismus (Deshayes, 1839)	+	P
Diplodonta orbellus (Gould, 1852)	+	
Kellia suborbicularis (Montagu, 1803)	+	P
Rochefortia aleutica Dall, 1899	Attu east	
R. tumida (Carpenter, 1864)	Attu east	
Cyclocardia crebricostata (Krause, 1885)	+	B
C. incisa (Dall, 1903)	Attu east	B
Astarte bennetti Dall, 1903	+	
A. rollandi Bernardi, 1858	+	
Clinocardium nuttalli (Conrad, 1837)	+	P
Serripes laperousi (Deshayes, 1839)	+	P
Mactromeris polynyma (Stimpson, 1860)	+	P
Macoma calcarea (Gmelin, 1791)	+	P
M. expansa (Carpenter, 1864)	Attu east	P
M. sp. cf. *M. obliqua* (Sowerby, 1817)	+	P
Cadella nuculoides (Reeve, 1844)	Attu east	P
Peronidia lutea (Wood, 1828)	+	P
Siliqua alta (Broderip & Sowerby, 1829)	+	P
S. patula (Dixon, 1789)	Attu east	P
Protothaca staminea (Conrad, 1837)	+	P
Saxidomus giganteus (Conrad, 1837)	Attu east	P
Liocyma fluctuosa (Gould, 1841)	+	
Hiatella arctica (Linnaeus, 1767)	+	
Mya arenaria Linnaeus, 1758	+	P
M. truncata Linnaeus, 1758	+	P
Thracia myopsis (Möller, 1842)	+	
Polyplacophora		
Leptochiton rugatus (Carpenter *in* Pilsbry, 1892)	+	
Schizoplax brandti (Middendorff, 1847)	+	
Tonicella lineata (Wood, 1815)	+	
T. rubra (Linnaeus, 1767)	+	
Juvenichiton saccharina (Dall, 1878)	+	
Placiphorella borealis (Pilsbry, 1893)	+	
Mopalia ciliata (Sowerby, 1840)	+	
Katharina tunicata (Wood, 1815)	Attu east	
Cryptochiton stelleri (Middendorff, 1847)	+	

far east as Amchitka (O'CLAIR, 1977). We have specimens from Amchitka as well as from Adak. Limpets were found at depths of 6–7 m on rocks and kelp blades. The Adak record is currently the easternmost limit of the species in the North Pacific.

Lottia digitalis (Rathke, 1833). This is an American limpet of the high intertidal zone. BAXTER (1987) recorded it as far west as Adak. During the 1987 *Alpha Helix* cruise, we found a population of very large individuals at North Point, Kiska. GOLIKOV & KUSSAKIN (1978) were inclined to doubt the record of *L. digitalis* from Avachin Bay, Kamchatka, which was based on empty shells. Accordingly, we regard Kiska as the westernmost record of *L. digitalis*. It is unlikely that these specimens represent a rare, fortuitous dispersal event as specimens collected in April 1974 are present in the collections of the University of Alaska Museum, Fairbanks, Alaska.

Acmaea mitra Rathke, 1833. In her compilation of Alaskan mollusks, FOSTER (1981) recorded an occurrence of this low intertidal and sublittoral limpet from Kiska. In our own surveys, we have found *A. mitra* only from Umnak east. Given the fact that the coralline-pavement habitats that are preferred by *A. mitra* are common and were carefully examined at all the islands visited, we are reasonably confident that *A. mitra* is absent or extremely rare west of Umnak. The Kiska record probably refers to *Erginus apicina* (Dall, 1879), a species very similar in appearance to the usually larger *A. mitra.* We therefore regard Umnak as the westernmost documented occurrence of this species.

Margarites pupillus (Gould, 1841). This common eastern Pacific trochid is abundant in the intertidal zone at Unalaska, and was found at depths of 6–7 m as far west as Umnak. Intensive searching in favorable low intertidal and sublittoral habitats on islands farther west failed to yield living or dead specimens.

Littorina aleutica Dall, 1872. This low-spired, often heavily sculptured species has often been confused with *L. sitkana* Philippi, 1846, but is in fact distinct (REID, 1989). It extends from the northern Kurile Islands to the Alaska Peninsula, and is common on most of the Aleutian islands we visited. Curiously, however, none of us has found it at Attu, and no material of *L. aleutica* is present in the large Aleutian holdings at the U.S. National Museum. Whether this absence represents a collecting artifact or a true absence is unclear.

Trichotropis cancellata Hinds, 1843. In Table 1 we have listed this species as extending continuously across the North Pacific from Asia to North America. In our collections, however, the species occurs only from Unalaska eastward. Although *T. cancellata* is reported from east Asia as well as from North America (GOLIKOV, 1986), the possibility that it has a discontinuous distribution cannot be eliminated on presently available evidence.

Opalia borealis (Keep, 1881). This large epitoniid is reported by DUSHANE (1979) as having its northern limit at Forrester Island in southeastern Alaska. We found living specimens at one intertidal and one shallow subtidal site

at Adak. These finds therefore represent a major westward extension of range for this species.

Nucella canaliculata (Duclos, 1832). It is remarkable that Soviet workers have not reported this common intertidal species from the Commander Islands or points farther west and south, because *N. canaliculata* is common at Attu (the westernmost of the Aleutians) and on all other islands we visited. O'CLAIR (1977) did not report the species from Amchitka, but we have found the species to be abundant there, and assume that O'Clair confused it with *N. lima* (Gmelin, 1791), which is also abundant throughout the Aleutians.

Nucella emarginata (Deshayes, 1839). Although we have not found this species in the Aleutians, we discuss it here in order to clarify the northern limit of this common eastern Pacific species. Elsewhere it will be shown (PALMER *et al.,* in press) that two species have been treated under the name *N. emarginata,* the southern or "true" *N. emarginata* from California and a northern species to which we shall, for the sake of convenience, refer as "northern" *N. emarginata.* DALL (1915) gave the range of *N. emarginata* (in the broad sense) as the southern Bering Sea and the Aleutian Islands south to northern Baja California. This range has been accepted by all later authors (*e.g.,* FOSTER, 1981; BAXTER, 1987). Inspection of the U.S. National Museum's collections upon which Dall based his conclusions show, however, that the Aleutian and Bering Sea records all refer either to *Buccinum baeri* or to *N. lima.* Palmer has collected *N. emarginata* at Yakutat, in southeastern Alaska. This is currently the northernmost valid record for the species.

Nucella lamellosa (Gmelin, 1791). In his review of North Pacific species of *Nucella,* DALL (1915) recorded *N. lamellosa* from the northeastern Pacific as well as from Sado Island in the Japan Sea. HABE (1958) followed Dall in accepting the western Pacific specimens as *N. lamellosa,* but GOLIKOV & KUSSAKIN (1962, 1978) regarded them as representing a distinct subspecies or species, *N. elongata* Golikov & Kussakin 1962. According to GOLIKOV & KUSSAKIN (1978), the range of this species is restricted to the southern Kurile Islands, Sakhalin, and the northern Sea of Japan. No specimens resembling *N. lamellosa* have been recognized by Soviet workers from the northern Kuriles, Kamchatka, or the Commander Islands (see also KUSSAKIN & coworkers, 1978). The previous western record for *N. lamellosa* is Adak (BAXTER, 1987). We have collected living specimens from as far west as Nizki, and have also found specimens at Adak and Umnak. The U.S. National Museum contains lots from Adak, Atka, and Unimak. Most of the specimens came from sublittoral rocks at depths of 6–7 m, but at Adak we found a few intertidal individuals. All the material we have seen from the Aleutians is strongly sculptured with axial frills, and the aperture is bordered by a thin lip unadorned with teeth. The smooth thick-lipped morphs so characteristic of the Puget Sound region apparently do not occur in southwestern Alaska.

Plicifusus stejnegeri (Dall, 1884). DALL (1884) described

this buccinid as *Strombella callorhina* var. *stejnegeri* from Bering Island in the Commander Islands, but he considered it possible that the new variety might be specifically distinct from his *S. callorhina* Dall, 1877, from the Pribiloff Islands. Soviet workers have justifiably considered it to be a distinct species, and have recorded it from the Commander and northern Kurile Islands (GOLIKOV & GULBIN, 1977). Our record from depths of 6–7 m at Nizki is believed to be the first reported occurrence of the species from Alaskan waters. *Plicifusus stejnegeri* differs from *P. kroeyeri* (Möller, 1842) by the higher spire, thicker outer lip, and especially by the axial ribs, which are much coarser and farther apart; *P. stejnegeri* differs from *P. callorhinus* by stronger and more closely spaced axial folds and by the higher spire.

Volutopsius pallidus Tiba, 1973. It is surprising that Dall and other early naturalists did not find this species in the Aleutians, for it is commonly found living in shallow subtidal waters, and also occurs as empty shells on beaches. We have specimens from as far east as Adak. In the Kuriles and in eastern Hokkaido, *P. pallidus* occurs at a depth of several hundred meters (TIBA, 1973; OKUTANI *et al.*, 1988). The smooth white shell distinguishes it from all other species of *Volutopsius*. We are persuaded that *V. pallidus* is not merely a pale deep-water variety of *V. middendorffi* (Dall, 1891), as OKUTANI *et al.* (1988) speculated.

Amphissa columbiana Dall, 1916. FOSTER (1981) recorded this large eastern Pacific columbellid from the Chiachi Islands off the south coast of the Alaska Peninsula and from the western Gulf of Alaska. BAXTER (1987) did not report the species from the Aleutians. In our survey, we found *A. columbiana* from Chuginadak eastward at depths of 6–7 m.

Mytilus californianus Conrad, 1837. In our surveys, this mussel was found to be common in the intertidal zone from Umnak eastward. We found a single small but extremely thick-shelled specimen at Seguam, and O'CLAIR (1977) reported a single specimen from Amchitka. All Aleutian specimens we have seen are remarkable for the very faint development of the radial folds that are so prominent in specimens in southeastern Alaska and farther south (see also VERMEIJ, 1989).

DISCUSSION

In his analysis of the shallow-water mollusks of Amchitka, O'CLAIR (1977) recognized 3 endemics (species restricted to the Aleutian and Commander islands), 5 Asian species, and 10 North American species among the 40 he collected from that island in the central Aleutians. As more biogeographical data have become available, however, it is increasingly clear that no molluscan species are endemic to the Aleutian-Commander arc. *Littorina aleutica,* for example, is now known to extend from the mainland coast of Alaska to the northern Kurile Islands (REID, 1989). *Astyris amiantis* (DALL, 1919), also regarded by O'Clair as endemic, occurs from mainland Alaska to the Kuriles
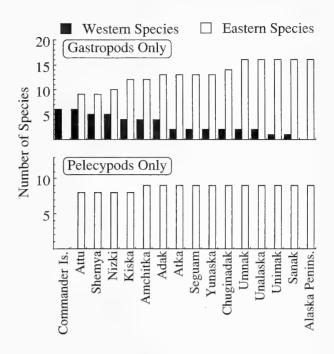
Figure 2

Patterns of disappearance of eastern and western Pacific species whose range boundaries occur somewhere within the Aleutian-Commander arc. Species occurring throughout the arc are not included. The height of the bar for each station along the arc indicates the number of species occurring at least that far east (solid bars) or west (open bars).

and to the island of Moneron in the Sea of Japan (GULBIN, 1983). Several of the species regarded by O'Clair as Asiatic (*Rhodopetala rosea, Onoba castanella* Dall, 1886, and *Cerithiopsis stejnegeri*) similarly have a continuous North Pacific distribution from North America to Asia. *Spiromoelleria quadrae* and *Littorina kurila* (as *L. atkana* Dall, 1896), classified as North American by O'Clair, again have continuous North Pacific ranges (BAXTER & McLEAN, 1984; REID, 1989).

Nevertheless, the evidence at hand indicates that the Aleutian chain contains the endpoints of range of many species. Of the 109 species (67 gastropods, 33 pelecypods, and 9 polyplacophorans) recorded in Table 1, 25 (16 gastropods, 8 pelecypods, and 1 polyplacophoran) reach their western limit somewhere in the Aleutians, and 6 (all gastropods) reach their eastern limits there (Figure 2). Attu (the westernmost of the Aleutians) is the western limit for 10 gastropods, 6 pelecypods, and 1 polyplacophoran, and the eastern limit for 1 gastropod. Some of these limits (especially those at Attu) will likely be changed as more collecting is done. Some of them may even shift with changing oceanographical conditions from year to year. Figure 2 shows that, with the exception of the range limits at Attu, the diminution of American species westward along the chain is almost exactly compensated by the addition of Asian species. At least one additional species (the pul-

Table 2

Distribution of planktonic and nonplanktonic development among biogeographical categories of Aleutian gastropods.

Category	Planktonic species	Nonplanktonic species	% species with planktonic larvae
Continuously ranging across North Pacific	12	24	33%
Western limits in Aleutians	4	7	36%
Eastern limits in Aleutians	0	5	0%

monate limpet *Liriola thersites*) reaches its western limit in the Commander Islands west of Attu (KUSSAKIN and coworkers, 1978). Species with continuous North Pacific distributions represent 71% (77 of 109 species) of the Aleutian shallow-water molluscan fauna.

The literature on geographical range in relation to dispersibility suggests that species with planktonic dispersal stages generally have larger geographical ranges than do species lacking such stages (see *e.g.*, HANSEN, 1978). Although there are exceptions, this relationship generally applies to tropical mollusks (see *e.g.*, PERRON & KOHN, 1985). At high latitudes, however, many species with non-planktonic larval stages nevertheless achieve very broad geographical ranges (ARNAUD, 1974; CANTERA & ARNAUD, 1984; HIGHSMITH, 1985), presumably because the larvae or even the adults are able to float or are transported on rafts of seaweed or wood.

Of the 52 gastropod species for which we were able to infer mode of larval dispersal, 35 have nonplanktonic stages and 17 have a planktonic phase (Table 1). Among the 35 species without planktonic larvae, 11 (31%) have eastern or western range limits within the Aleutian-Commander arc. The comparable figure for planktonically dispersing species is 29% (5 of 17 species), a number not significantly different from the 33% for nonplanktonic dispersers (*G*-statistic with Yates Correction, *P* > 0.10). The bivalves show a similar pattern; 20% of the species without planktonic larvae have range endpoints within the Aleutian-Commander arc, compared to 25% with planktonic larvae.

These data imply that, although there is a slight tendency for planktonic dispersal to be associated with a continuous east–west distribution across the North Pacific, the water barriers between islands in the Aleutian-Commander chain are nearly as effective for planktonically dispersing species of gastropods as for species that lack planktonic life stages. This interpretation, however, may be somewhat complicated by the fact that the incidence of nonplanktonic development among species within western limits in the Aleutians (7 of 11 species, 65%) is lower than that among species reaching their eastern limits in the

Aleutians (5 of 5 species, 100%) (Table 2). The number of species is too small to determine if this difference between American and Asian gastropods is statistically significant. Future studies may have to take geographical origin into account in analyses of the relationship between range and dispersibility. Too few species had range endpoints within the Aleutian-Commander arc to conduct this analysis for pelecypods.

It is surprising that the Aleutian-Commander arc presents a barrier for many northeastern Pacific species with pelagic larval stages. The westward-flowing Alaska Stream along the south coast of the Alaska Peninsula and the Aleutian Islands (MCALISTER & FAVORITE, 1977) can potentially transport pelagic larvae of North American species westward. Moreover, there appears to be no obvious thermal or other oceanographical barrier along the island arc that could serve to limit the range of pelagically dispersing species. MILLER & ESTES (1989) described a similar paradox for the large bull kelp *Nereocystis luetkeana*, which has been seen living as far west as Umnak but which washes ashore (after westward transport) as floating plants at Attu and even in Hokkaido.

The possibility exists that the biogeographical barriers along the mainland coasts of Alaska and Siberia are just as effective, and act in the same way, as do the inter-island barriers in the Aleutian-Commander arc. Because detailed knowledge of range endpoints of species is lacking in many cases, especially in western Alaska, this interesting possibility cannot be examined further at this time.

In our analysis, we evaluated dispersibility of species by correlating inferred larval type with the distribution across barriers along a specific island arc, in which the number and size of such barriers are known. This method, which was also used by VERMEIJ (1987) in a study of over-water dispersibility of gastropods across water barriers in the tropical Pacific, differs from the more conventional method of comparing larval type against the total geographical ranges of species, as was done by HANSEN (1978) and by many others. The disadvantage of assessing dispersibility by means of whole ranges is that the precise range limits are often poorly known. The latitudinal and longitudinal extent of range, however, is very sensitive to the precise delimitation of distributional endpoints. By focusing on whether species can cross specific barriers, this problem is alleviated at least to some extent.

That the water barriers in the North Pacific have been more or less effective for millions of years is implied by the fact that a large number of eastern Pacific genera, most of which are known back to Oligocene time, are unknown as fossils or as living species in the western Pacific. Examples of such genera in the Aleutian fauna include *Opalia, Amphissa, Mytilus* (*Pacifimytilus*) (for *M. californianus*), and *Crassidomus* (for fossil records see BERNARD, 1986; KAFANOV, 1987). Whatever the explanation for the effectiveness of the barriers, the phenomena responsible for the barriers should be observable throughout much of the Neogene.

It is possible that recruitment is so infrequent that plank-tonically dispersing species cannot maintain populations for long periods of time. This is clearly not a problem for sea urchins of the genus *Strongylocentrotus* (ESTES *et al.,* 1989), but for other Aleutian invertebrates successful set-tlement of pelagic larvae may be a rare event. This kind of recruitment limitation has been proposed as an expla-nation for fluctuating northern range limits and for heavily adult-biased population structures of invertebrates in northern European seas (LEWIS *et al.,* 1982). Until more is known about reproductive patterns and the oceano-graphical conditions upon which they depend, however, an evaluation of such a hypothesis for the Aleutian fauna is impossible.

ACKNOWLEDGMENTS

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Burrowing Times of *Donax serra* from the South and West Coasts of South Africa

by

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Abstract. Burrowing times of winter acclimated populations of *Donax serra* from the west and south coasts of South Africa were compared at three experimental temperatures in an effort to explain observed zonation patterns. The west coast population burrowed slower than the south coast population at 10°C and 15°C, but at the same rate at 20°C. Burrowing time decreased at increased temperatures. The burrowing rate index ranged from 5 to 14, indicating that *D. serra* is among the most rapidly burrowing bivalves examined to date. The results indicate no physiological adaptation of burrowing rate to temperature between populations.

INTRODUCTION

Members of the bivalve genus *Donax* are common inhabitants of open coastal sandy beaches throughout the warm-temperate and tropical regions of the world (ANSELL, 1983). In response to the dynamic nature of these environments, most species are tidal migrants, burrowing rapidly into the sediments of the beach face between wave swashes. STANLEY (1970) considers members of the genus *Donax* to be among the most rapidly burrowing bivalves.

Of the nine species of *Donax* inhabiting the southern African region (KILBURN & RIPPEY, 1982), *Donax serra* Röding is the best studied (BROWN *et al.,* 1989). Its distribution extends from the Kunene River at the northern border of Namibia into western Transkei, South Africa (Figure 1). Throughout this range, it is capable of maintaining large populations with biomasses of up to 7000–9000 g (dry wt.)/m (McLACHLAN, 1977; HUTCHINGS *et al.,* 1983). Temperature regimes along the west and south coasts of southern Africa are markedly different, the west coast being dominated by the cold waters of the Benguela upwelling region, while the south coast is influenced by the warm waters of the Agulhas current. Differences in zonation pattern between populations inhabiting the two coasts have also been reported. *Donax serra* is found in low intertidal and shallow subtidal zones along the west coast (HUTCHINGS *et al.,* 1983), while along the south coast it is found in the mid-intertidal zone (McLACHLAN *et al.,* 1979; DONN *et al.,* 1986).
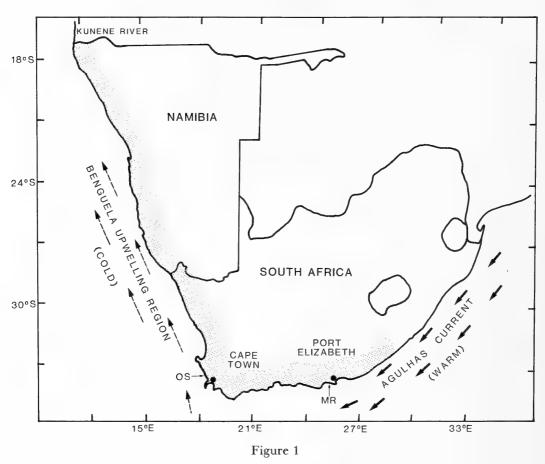
Members of the genus *Donax* rely on their ability to burrow rapidly in order to maintain their position on highly dynamic beaches (TRUEMAN, 1971). The burrowing mechanisms used by *D. serra* have been described in detail by TRUEMAN & BROWN (1985). McLACHLAN & YOUNG (1982) have shown that reduced temperatures negatively affect burrowing rate in a south coast population. One would expect a population inhabiting colder waters to have evolved mechanisms to compensate for lower temperatures. Burrowing time is an easily measured parameter relating directly to the bivalve's response to its environment and is important in maintaining zonation patterns. The objective of this study was to compare the burrowing times of south and west coast populations of *D. serra* and to assess any temperature adaptation between the two populations.

MATERIALS AND METHODS

Individuals of *Donax serra* were collected from Maitlands River beach near Port Elizabeth (hereafter referred to as the south coast population) and from Ou Skip north of Cape Town (west coast population) during May–June 1989 (Figure 1). Average expected sea surface temperatures at this time were 17°C for Port Elizabeth and 14°C for Cape Town (CHRISTENSEN, 1980). Annual temperature range for Port Elizabeth is 15–21°C, and 12–15°C at Cape Town (CHRISTENSEN, 1980). Individuals ranged in length from 15 to 75 mm. In the laboratory, bivalves were allowed to burrow into natural Maitlands River beach sediments covered by aerated, flowing seawater and acclimated at 15°C for 36 H prior to initiating the experiment.

Three experimental temperatures, 10, 15 and 20°C, were used, covering the range of temperatures experienced by

Figure 1

Map of Southern Africa showing distribution of *Donax serra* (shading) and location of sampling sites at Ou Skip (OS) and Maitlands River (MR). Also included are the positions of the Agulhas Current and the Benguela upwelling region.

the species in nature. Animals were transferred directly from the holding tank and placed into experimental chambers. Burrowing time was defined as the time from initiation of digging by the foot until complete burial or until all burrowing activity stopped (McLachlan & Young, 1982). Each animal was allowed to burrow three times and the mean burrowing time determined. At least 30 animals covering the full range of sizes from each site were tested at each temperature.

After having burrowed three times, each individual of *Donax serra* was measured to the nearest 0.1 mm in anterior–posterior length and blotted wet weight determined to 0.01 g. The burrowing rate index (BRI), defined as the cube root of wet weight (g) divided by the burrowing time (s) multiplied by 100 (Stanley, 1970), was calculated.

RESULTS
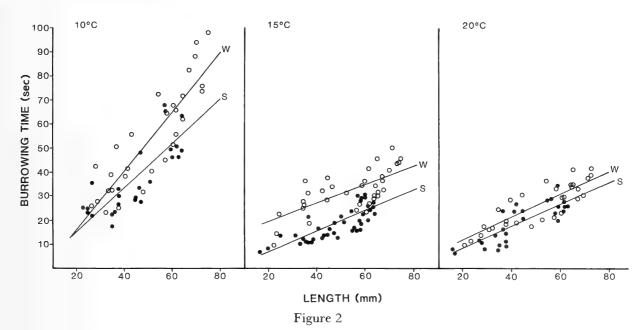
Most animals burrowed completely. Only a few of the largest west coast individuals of *Donax serra* remained partially (≤10%) exposed when burrowing activity ceased.

Linear regressions of mean burrowing time against length were determined for each population at the three temper-

atures (Figure 2) and compared between sites using the dummy-variable regression approach (Kleinbaum & Kupper, 1978) (Table 1). Significant differences were detected between the population regression lines at 10 and 15°C, but not at 20°C. Burrowing time decreased with increasing temperatures for the west coast population, *i.e.*, burrowing rate increased. The south coast population showed a decrease in burrowing time between 10 and 15°C, but not between 15 and 20°C.

Analysis of the burrowing rate index (Stanley, 1970) yielded similar results. BRI was independent of *Donax serra* length at all temperatures. A one-way analysis of variance on BRI for *D. serra* at each temperature (Table 2) indicated significant differences between populations. BRI increased with temperature in the west coast population. In the south coast population, BRI increased markedly between 10 and 15°C, but decreased slightly between 15 and 20°C.

DISCUSSION

Stanley (1970) determined the BRI at ambient environmental temperatures for over 60 western Atlantic bivalve

Figure 2

Mean individual burrowing time (sec) versus length (mm) for west (W) and south (S) coast populations of *Donax serra* at three experimental temperatures. ○ west coast; ● south coast.

species including two species of *Donax*. BRI for these species ranged from 0.01 to 20; species with a BRI greater than two were classified as rapid burrowers and greater than six as very rapid burrowers. *Donax denticulatus* and *D. variabilis* scored 17 and 7, respectively, on this scale. Recently, TRUEMAN & BROWN (1989) have given a BRI for west coast *D. serra* of 6.9. This corresponds well with the BRIs determined in this study, which span the range determined for the other two *Donax* species, indicating that *D. serra* is one of the most rapid burrowers of all species of bivalve examined to date. Furthermore, we have shown that the BRI is influenced by temperature. When comparing BRIs, care must be taken to state whether the measurements were done at ambient environmental tem-

peratures (ecological differences) or at constant experimental temperatures (physiological differences).

McLACHLAN & YOUNG (1982) found that summer acclimated *Donax serra* burrowed more slowly at 10°C than winter acclimated animals, indicating seasonal acclimation in south coast populations. In light of this we expected that either both populations would burrow at the same rate, *i.e.*, no adaptation, or that the west coast population would have adapted to the colder temperatures and burrowed more rapidly. Our results show that west coast populations burrow more slowly than south coast populations when acclimated to the same temperature.

One possible explanation for differences in burrowing time may be differences in shell morphology. Both shell obesity (width-to-height ratio) (TRUEMAN *et al.*, 1966) and shell elongation (STANLEY, 1970) have been shown to affect the rate at which bivalves burrow. Preliminary results indicate differences in shell morphology between south and west coast populations of *Donax serra*. These differences and their effect on behavior will be investigated in sub-

Table 1

Comparison of burrowing time vs. length regressions for south and west coast populations of *Donax serra* at three test temperatures. * $P < 0.05$.

	Intercept	Slope	r^2	n
T = 10°C				
South coast	−2.312 [n.s.]	0.904 [*]	0.683	32
West coast	−8.791	1.234	0.790	30
T = 15°C				
South coast	−1.672 [*]	0.428 [n.s.]	0.643	50
West coast	11.512	0.387	0.497	36
T = 20°C				
South coast	−0.926 [n.s.]	0.459 [n.s.]	0.697	33
West coast	2.490	0.474	0.707	29

Table 2

Comparison of burrowing rate index (BRI) of south and west coast populations of *Donax serra* at three temperatures. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Temperature	South coast	West coast	Significance level
10°C	6.35	5.22	**
15°C	13.85	8.97	***
20°C	12.52	10.42	**

Table 3

Comparison of burrowing times (seconds) for three size classes of summer and winter acclimated *Donax serra* from the south and west coasts. Data for summer acclimated animals taken from McLachlan & Young (1982).

	McLachlan & Young (1982)		Present study	
Coast	S	S	S	W
Acclimation	summer (21°C)	winter (16°C)	winter (15°C)	winter (15°C)
Test temperature	20°C	10°C	10°C	10°C
Length (mm)				
15	9	16	11	10
25	13	23	20	22
50	23	35	43	53

sequent papers. Similarly, Trueman & Brown (1989) found that *Bullia digitalis* from the west coast burrowed more slowly than individuals from south coast populations, but ascribed this to differences in physiological condition.

Water temperatures along the west coast are considerably colder than along the south coast (Christensen, 1980). In addition, west coast populations of *Donax serra* burrow more slowly than south coast populations at the same temperatures. Therefore, in their natural habitats, the two populations will differ markedly in burrowing rate (Table 3). As both coasts experience similar wave climates (Rossouw, 1984), swash periods and frequencies should be similar. McLachlan & Young (1982) estimated that burial times must be less than 48 sec to prevent *D. serra* from being dislodged by subsequent swashes. Clearly, south coast populations can burrow sufficiently fast to maintain their position on the beach face, whereas the west coast populations would not have sufficient time to burrow at the peak of the swash before being carried down the beach by the backwash. This is indeed the pattern reflected in their observed field distributions; *D. serra* in the south coast inhabit the intertidal zone (McLachlan *et al.*, 1979; Donn *et al.*, 1986), while on the west coast they are found at or below spring low water (Hutchings *et al.*, 1983).

We conclude that there is little evidence for physiological adaptation of burrowing time to temperature between south and west coast populations of *Donax serra* and suggest that the lower than expected burrowing rates of the west coast population may be a result of morphological differences between the two. Furthermore, the combination of slower burrowing rates and lower environmental temperatures may be responsible for differences in zonal differences on the shore.

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Chemoautotrophic Sulfur Bacteria as a Food Source for Mollusks at Intertidal Hydrothermal Vents: Evidence from Stable Isotopes

by

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Abstract. Stable carbon and nitrogen isotope measurements indicate that limpets (*Lottia limatula*), which normally graze on algae, have diets consisting predominantly of chemoautotrophic sulfide-oxidizing bacteria at southern California intertidal hydrothermal vents. Suspension-feeding mussels (*Mytilus edulis*) at the intertidal vents show only minor inclusion of the chemoautotrophic bacteria in their diet. This is the first evidence from stable isotopes that geothermally driven primary production can be of major importance to intertidal grazers.
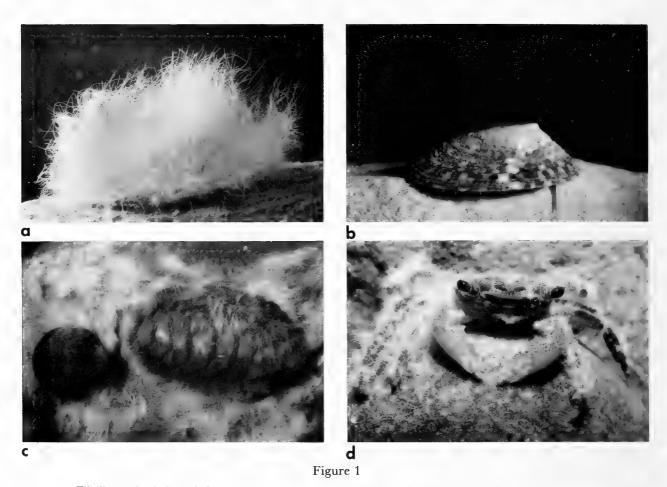
INTRODUCTION

The discovery of dense animal and bacterial populations at deep-sea hydrothermal vents, living in the absence of sunlight, suggested that these biological communities were supported locally by chemosynthetic vent bacteria rather than minimal amounts of photosynthetically produced material drifting down from the sunlit zone. Much evidence has since been gathered confirming the hypothesis that chemoautotrophic bacteria are the primary producers at deep-sea vents. These bacteria support a community of invertebrate grazers (*e.g.,* limpets), suspension feeders (*e.g.,* clams, mussels), predators and scavengers (*e.g.,* crabs), and may also supply organic carbon to macroinvertebrates through symbiotic associations (RAU, 1985; HESSLER & SMITHEY, 1984; CAVANAUGH, 1983; FELBECK & SOMERO, 1982; WILLIAMS *et al.,* 1981).

Vent bacteria produce biomass and obtain energy from oxidation of geothermally reduced compounds (*e.g.,* hydrogen sulfide, ammonia, and hydrogen) in vent waters (JANNASCH & WIRSEN, 1979). Sulfide-oxidizing bacteria appear to be among the most conspicuous primary producers at vents (RUBY *et al.,* 1981). Consumption of sulfide-oxidizing bacteria occurs wherever sulfide levels are high enough to support chemosynthesis. In most of these habitats, however, the sulfide is biologically produced by sulfate-reducing bacteria (SPIES & DESMARAIS, 1983) rather than being geothermally produced as in deep-sea vents. The possibility that geothermally driven chemosynthesis is important for some organisms in habitats other than deep-sea vents has been suggested. STEIN (1984) reported the partial contribution of sulfide-oxidizing bacteria to the diet of black abalone *Haliotus cracherodii* Leach, 1814, at coastal hydrothermal vents. Ciliates, flagellates, and aquatic insect larvae consume sulfide-oxidizing bacteria in terrestrial hot springs (LACKEY *et al.,* 1965). Thus, geothermally driven primary production is not unique to deep-sea vents, and may contribute to community biomass wherever hydrothermal vents occur in the photic zone.

Little is known of the relative nutritional importance of chemosynthesis versus photosynthesis at sunlit vents. STEIN (1984) observed that in addition to black abalone, several species of limpets appeared to graze on benthic mats of bacteria (the most conspicuous species of the bacterial assemblage resembled *Thoithrix* Winogradsky, a known sul-

Figure 1

a. File limpet *Lottia limatula* from intertidal vent, with dense growth of filamentous sulfide-oxidizing bacteria on shell. b. File limpet collected 10 m from nearest vent. c. Mossy chiton *Mopalia muscosa* (Gould, 1846) and black turban snail *Tegula funebralis* (A. Adams, 1855) on bacteria-covered rock at intertidal vent. d. Shore crab *Pachygrapsus crassipes* from intertidal vent, with bacterial growth on exoskeleton.

fide oxidizer) at intertidal hydrothermal vents located at White Point, southern California. In our study, closer examination of intertidal vents in the same area where STEIN (1984) worked subtidally revealed the presence of numerous common intertidal mollusks and crabs. The hard body surfaces (shell and exoskeleton) of many individuals at these vents were covered with a thick growth of attached filamentous sulfide-oxidizing bacteria (Figure 1). These bacteria grow only in the immediate vicinity of vents where sulfide levels are high enough to support chemosynthetic production of biomass, and indicate that animals covered with bacteria spend a considerable amount of time bathed in the warm, sulfide-rich vent effluent (up to 28°C and 141 μM/L; STEIN, 1984).

These observations suggested that vent bacteria might form a substantial portion of the diets of some intertidal macroinvertebrates. We examined this possibility for two species of intertidal mollusks that occur commonly at and away from vents. The file limpet *Lottia limatula* (Carpen-

ter, 1864) is a benthic grazer, while the common mussel *Mytilus edulis* Linnaeus, 1758, was chosen as a representative suspension feeder.

MATERIALS AND METHODS

Possible dietary sources were investigated by measuring the stable carbon and nitrogen isotopic composition (^{13}C/^{12}C and ^{15}N/^{14}N ratios) of both animal tissues and their potential food items. This approach was used because, if stable isotope ratios of different food types differ substantially, these isotopic ratios can be used as natural markers to trace dietary sources, as the ratios change little when assimilated into animal tissue (DENIRO & EPSTEIN, 1978, 1981). Use of this method in other studies has indicated a trophic link between deep-sea vent bacteria and deep-vent consumers (RAU, 1985; RAU & HEDGES, 1979).

Samples were taken from intertidal vent (*i.e.*, within 10 cm of a vent opening) and non-vent (at least 10 m from

Table 1

$\delta^{13}C$ and $\delta^{15}N$ values for vent and non-vent organisms and their potential food sources. Sample size (n) for animals = the number of individuals analyzed. Three samples of vent bacteria and one algal sample were analyzed. Values are given as the mean ± SE if n is greater than 1.

Organism	n	$\delta^{13}C$	$\delta^{15}N$
Vent			
Bacteria	3	-31.0 ± 0.3	-4.1 ± 1.3
Lottia limatula	2*	-30.4	-1.3
Mytilus edulis	3	-16.6 ± 0.7	$+6.4 \pm 1.0$
Non-vent			
Benthic algae	1	-15.1	$+6.8$
Lottia limatula	3*	-15.5	$+6.3$
Mytilus edulis	1	-15.3	$+8.6$

* These limpets were analyzed as one sample.

the nearest detectable vent opening) sites at White Point in southern California. Vent openings were easily detected because the rocky substrate surrounding an opening is devoid of algal growth but covered with dense, off-white mats of sulfur bacteria.

Vent bacterial and non-vent benthic algal samples were scraped from rocks. Limpets were collected and kept live in 25-μm filtered seawater to allow for gut evacuation, so the isotopic composition of the whole body could be determined without contamination from ingested but unassimilated material. Mussels were collected and their foot and mantle tissues were dissected out for analysis, to avoid contamination by gut contents. All samples were lyophilized, ground to powder, treated with 1 N HCl to remove carbonate, and lyophilized again before combustion (NORTHFELT *et al.,* 1981). The resulting CO_2 and N_2 were separated cryogenically and their volumes determined manometrically prior to mass spectrometric analysis. The isotopic compositions are expressed in the usual δ notation where $\delta X = [\{R(sample)/R\ (standard)\} - 1] \times 1000‰$ and $X = {}^{13}C$ or ${}^{15}N$, $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$, and the standard = PDB belemnite or atmospheric N_2, respectively, for carbon and nitrogen (RAU, 1985).

RESULTS AND DISCUSSION

The carbon isotope ratios reported in Table 1 suggest that the diet of intertidal vent limpets consisted predominantly of sulfide-oxidizing bacteria. The $\delta^{13}C$ values of vent limpets match those of vent bacteria. The $\delta^{13}C$ values of non-vent limpets, in contrast, were decidedly less negative than those of the vent limpets, and are similar to those of their likely food source, photosynthetic algae encrusting the rocks on which they live.

Carbon isotope ratios of mussels living near and away from the intertidal vents (Table 1) suggest that the vent mussels are using only small amounts of vent bacteria as

a food source. The $\delta^{13}C$ values for vent mussels are only about 1‰ more negative than those for non-vent mussels. This 1‰ difference contrasts with the 16‰ difference in the $\delta^{13}C$ values between the vent bacteria and the non-vent algae, which may be taken as the difference between the chemosynthetically and photosynthetically derived food sources in the area. If the photosynthetically derived food used by the mussels had $\delta^{13}C$ values similar to the benthic algae we analyzed (Table 1), the mussel $\delta^{13}C$ values suggest that more than 95% of the vent mussel food was not derived from vent bacteria. Water column concentrations of suspended bacteria detached from vent bacterial mats were not measured in this study, but are presumably high near vents because many suspended filaments of mat bacteria are visible to the naked eye over vent openings (especially when wave action detaches parts of the attached mat). Presumably, a suspension feeder, like *Mytilus edulis*, that is situated directly over a vent must entrain some bacteria in its feeding current. Most of these bacteria may subsequently be sorted out and rejected in favor of plankton in non-vent water that mixes with vent effluent.

Nitrogen isotope measurements may also provide information on trophic relationships. For deep-sea vent and other marine organisms, the $\delta^{15}N$ values increase approximately 2–3‰ with each change in trophic level (RAU, 1985). Our measurements for intertidal vent limpets are in good agreement with this trend. The $\delta^{15}N$ value for limpets is 2.8‰ higher than that for vent bacteria (Table 1), strengthening the conclusion that the bulk of vent limpet diet consists of vent bacteria. The unusually low $\delta^{15}N$ value for vent bacteria may be an indication of bacterial N_2 fixation as a vent nitrogen source, rather than a biologically cycled nitrogen source (*e.g.,* nitrate), which would have a more positive $\delta^{15}N$ value (RAU, 1985). On the other hand, it is also possible that vent water contains an ${}^{15}N$-depleted organic source of nitrogen. For non-vent control limpets, the $\delta^{15}N$ values are close to that of their algal food source but do not show the slight rise predicted with a change in trophic level. Nevertheless, the values are consistent with a non-vent photosynthetically generated food source (RAU, 1985).

The $\delta^{15}N$ values for vent and non-vent mussels are consistent with our conclusion that vent mussels use vent bacteria as only a minor food source.

According to STEIN (1984), mollusks are the only macroinvertebrates occurring commonly at subtidal White Point hydrothermal vents. At the littoral zone vents examined in our study, mollusks are the dominant macroinvertebrates, but two arthropods, the striped shore crab *Pachygrapsus crassipes* Randall, 1839 (Figure 1d) and the blue-clawed hermit crab *Pagurus samuelis* (Stimpson, 1857), are also common. It is therefore possible that these and other shallow-water marine macroinvertebrates, in addition to file limpets and black abalone, use vent bacteria as an important food source. Also, the assemblage of tiny organisms associated with mats of coastal vent bacteria (*e.g.,* copepods, flatworms, polychaetes, flagellates), and

the bacteria themselves, have not yet been fully characterized. Because of easy access, there is great potential to investigate further the nature of trophic relationships within these shallow-water hydrothermal vent communities.

Our study is a first account of both carbon and nitrogen stable isotope measurements indicating that geothermally driven production of biomass is of major nutritional importance for certain consumers, even in the sunlit zone where photosynthesis dominates.

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Survival, Growth, and Fecundity of the West Indian Topshell, *Cittarium pica* (Linnaeus), in Various Rocky Intertidal Habitats of the Exuma Cays, Bahamas

by

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Abstract. The West Indian topshell, *Cittarium pica*, is the most intensively fished intertidal marine snail of the West Indies. However, its population dynamics are poorly known. Different habitat types, varying in degree of wave exposure, were chosen to study survival, growth, and fecundity of unexploited Bahamian *Cittarium* populations.

Several aspects of *Cittarium* life history differed between habitats. Snails inhabiting wave-exposed habitat had lower rates of survival and growth and a smaller average shell size than snails of sheltered habitat. Wave-exposed habitat had higher *Cittarium* densities and higher predatory gastropod densities than more sheltered habitats. Dead shells recovered from wave-exposed habitat showed a higher proportion of lethal damage due to shell-drilling and crushing. Size of maturation was smaller and fecundity was lower for snails residing in wave-exposed habitat.

Differences in population structure between habitats were attributed to differences in survival and growth and not to temporal differences in recruitment. Low *Cittarium* abundance in sheltered habitat, despite high survival rate, suggested a lower level of recruitment to such habitat.

INTRODUCTION

The West Indian topshell, *Cittarium pica* (Linnaeus, 1758) (=*Livona pica*) has been harvested since pre-Columbian times (GOULD, 1971) and is the largest shallow-water trochacean gastropod of the western Atlantic, often reaching a shell diameter of 10 cm. This herbivorous snail is sedentary and is found in a variety of rocky intertidal habitats throughout the West Indies. The snail has rarely been found in southern Florida (ABBOTT, 1976) and suffered recent extinction in Bermuda (CLENCH & ABBOTT, 1943).

Information on the biology of *Cittarium* is limited. The snail's anatomy (CLENCH & ABBOTT, 1943; GRAHAM, 1965), shell ultrastructure (WISE & HAY, 1968a, b), and flight response (HOFFMAN & WELDON, 1977) have been

described. Only one study has dealt with *Cittarium* population dynamics (RANDALL, 1964).

The objectives of the present study were to quantify the degree to which survival, growth, and fecundity are habitat dependent and to determine whether low population densities in wave-sheltered habitats are due to low recruitment or low post-recruit survival.

MATERIALS AND METHODS

Field work was conducted between August 1984 and January 1985 in the Exuma Cays Land and Sea Park, between Soldier Cay and Waderick Wells Cay, Bahamas (Figure 1). The park spans a total of 35 km of the Exuma island chain and is 13 km wide. Much of the intertidal zone is rocky and offers potential habitat for *Cittarium*. With winds predominantly from the southeast, the eastern shores of the islands are exposed to ocean swell from the Exuma Sound, while the western shores remain sheltered.

Four categories of rocky habitat were distinguished along
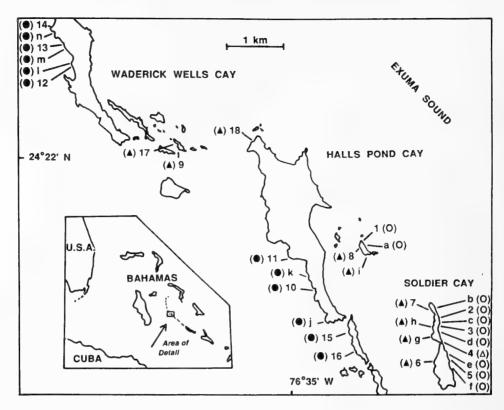
Figure 1

Map of the study area in the Exuma Cays Land and Sea Park, Bahamas, showing the size-frequency collection sites (a–n) and the tag-recapture sites (1–14). Estimates of population density were obtained at all numbered sites except 4 and 13. Habitat types are EXP (O), EXSS (△), INT (▲), and SH (●).

this gradient of wave exposure. Exposed (EXP) habitat generally showed a 30° slope through the splash zone and a nearly vertical drop of 1–1.5 m from the edge of the low tide bench (Figure 2). One-meter-high waves were common. The substrate in this habitat was highly rugose and pitted. The sea urchin *Echinometra lucunter* and the alga *Padina* (*Padina* sp.) were abundant on the low tide bench. In the upper splash zone, the limpet *Acmaea leucopleura* was abundant. EXP habitat was predominant on eastern shores.

Exposed shallow-sloping (EXSS) habitat contrasted with EXP habitat in having a shallow-sloping seabed below the low tide level. EXSS habitat was rare and was the only other habitat type distinguished on wave-exposed shores. Within the study area, EXSS habitat was found on Soldier Cay and Halls Pond Cay.

Intermediate (INT) habitat was found in channels between the islands where the effects of ocean swell were still present and wave heights of up to 0.5 m were common. The habitat had no distinguishing topography, with intertidal slopes varying widely. *Echinometra lucunter* was less abundant than in EXP habitat.

Sheltered (SH) habitat was found on the shallow leeward side of the islands where waves were usually less

than 0.2 m. Typical were the presence of an undercut in the intertidal zone (Figure 2) and less rugosity than in EXP habitat. The undercut caused the intertidal zone of this habitat type to be shaded for large parts of the day. *Echinometra lucunter* was rare, and the lower-intertidal zone was covered by a spongy, sand-laden algal mat. The isopod *Ligia* sp. descended in great numbers into the intertidal zone at low tide.

Densities per unit area were obtained for *Cittarium* and predatory gastropods of the genera *Thais* and *Purpura* (thaids) at four EXP, six INT, and six SH sites. At each site, 10 m² of habitat was sampled over the zone of highest snail density, following HUGHES (1971). ANOVA *F*-tests were utilized to compare snail densities between habitat types (KLEINBAUM & KUPPER, 1978). All statistical tests presented in this report are two-tailed tests. Unless otherwise stated, statistical comparisons of parameters between habitat types were not done by pooling recoveries between sites but by considering each site within a habitat class as a single replicate.

Population size-frequency collections were made during the peak of the reproductive season (DEBROT, 1990) at 14 sites in August 1984. Of these, six were EXP, three were INT, and five were SH sites. Sample sites were chosen to

be at least 150 m apart unless they were separated by a sandy beach that prevented dispersal of postlarval individuals of this snail. Distribution of the snails was confined to a narrow, 1–2 m wide intertidal zone, which greatly facilitated sampling. At each site all snails were collected, by snorkeling and wading, from as many meters of coast as was necessary to fill a standard net bag.

To quantify survival and growth, a transplant experiment involving 14 sites was done. A total of 600 small snails with a mean shell width of 22.8 ± 7.2 mm (95% confidence interval) were collected from the ocean side of Soldier Cay. Shell width was defined as the widest diameter across the base of the shell. Oval 2 × 5 mm plastic tags were attached to the dry shell surfaces of the snails using marine epoxy cement (Underwater Patching Compound, Pettit Paint Co., Spring Valley, CA). One hundred of the snails were double-tagged to estimate tag shedding by the method of GULLAND (1963). The snails were set out at four EXP, one EXSS, four INT, and five SH sites. Forty snails were released at each site except site 4 (the only EXSS site) where 80 snails were released. In addition, a total of 101 large (80.0 ± 13.8 mm) animals were released at three EXP and three SH sites. After approximately 168–174 days at liberty, all survivors that could be found within a 20-m radius from the point of release at each site were collected.

Handling mortality was estimated by recording the live tagged snails seen at each site three days after release and assuming that all handling mortality takes effect within the first three days. After a period of time, Δt, the fraction of snails recovered from the total number of snails released can be expressed as $RT_t = RS_t H$, where RS_t is the recovery rate after period Δt, assuming no handling mortality, and H is handling survival. If natural mortality during the three-day period is assumed negligible, then handling survival can be calculated as:
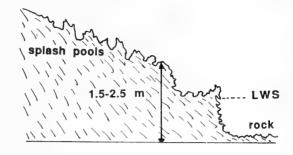
$$H = RT_t/RS_{t-3} \tag{1}$$

where RS_{t-3} is the fraction recovered from snails seen alive three days after release. Estimates were tested for differences with 100% handling survival using a χ^2 goodness-of-fit test (SOKAL & ROHLF, 1981).

Recovery efficiency was defined as the percentage of tagged snails recovered from the site after repetitive sampling. At each site, tagged snails were removed during low tide events until a collection yielded no recoveries. Recovery efficiency was calculated separately for small and large snails using the DeLury method (RICKER, 1975) on data pooled between SH, INT, and EXP sites.

After a period at liberty, expected tagged-snail population densities should be highest near their point of release and should decrease with increasing distance from the release point, assuming random movements. Emigration was, therefore, quantified by fitting a curve to the number of recaptures as a function of distance from the point of release (POOLE, 1974). Of the several curves tried, log-normal curves of the form $Y = a - B \ln(X)$ where Y is

(a) EXP

(b) SH
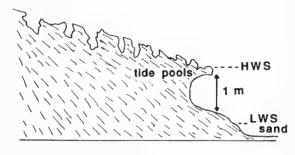
Figure 2

Vertical shore profiles for (a) EXP and (b) SH habitat types. LWS ≡ low tide level, HWS ≡ high tide level (spring tides).

the number of recaptures at distance X (m) each side from the point of release, provided the best fits to the dispersal data. Data for habitats with recoveries at multiple sites were pooled and weighted for equal representation of each site.

Survival for the period Δt for snails of size i was then calculated as:

$$S_{i,t} = R_{i,t}/(N_{i,0}TaF_iEH) \tag{2}$$

where $R_{i,t}$ is the number of snails of size i that were recaptured at the end of the period Δt, $N_{i,0}$ is the number of snails of size i that were released, Ta is the fraction of tags still attached, F_i is the fraction of snails of size i inside the study site that were also found, E is the fraction of snails still inside the study site, and H is handling survival. Losses due to fishing mortality were considered negligible because of the remoteness of the area and the abundance of other attractive fishing sites in the area. Survival estimates were expressed in terms of annual percent survival (RICKER, 1975). Data were non-normally distributed so that these estimates were compared between habitats using the Kruskal-Wallis test (SOKAL & ROHLF, 1981).

Dead shells (either empty or occupied by a hermit crab) were collected to assess the relative importance of different agents of natural mortality. To avoid double-counting, only relatively fresh shells with shiny nacre and intact spire

Table 1

Population densities of *Cittarium* and its molluscan predators (thaids) in three habitat types: exposed (EXP), intermediate (INT), and sheltered (SH).

Habitat type	Number of sites sampled	Density (numbers/m²)			
		C. pica		Thaids	
		Average	Range	Average	Range
EXP	4	6.0	3.6–8.5	0.7	0.3–1.1
INT	6	2.3	0.2–5.9	0.0	—
SH	6	0.1	0.0–0.5	0.0	—

Table 2

Cittarium releases, percent recovery, and percent handling survival (H) for small ($\bar{x} = 22.8$ mm) and large ($\bar{x} = 80.0$ mm) snails.

	Total releases		Seen 3 days after release		
	Number released	Percent recovered	Number seen	Percent recovered*	H
Small snails	596	16.4	337	17.5	94.0
Large snails	101	23.8	63	27.0	88.0

* Percent recovered from those snails that were observed to be alive 3 days after release (RS_{1-3} in equation 1).

tips were used. Shells with extensive breakage were assumed to have died from crushing predation. Shells with either lethal drilling or both lethal drilling and lethal shell breakage were assumed to have died due to drilling. Comparisons of the relative importance of various causes of natural mortality between habitats were done using the χ^2 goodness-of-fit test. The Fisher-Irwin test (χ^2 test-equivalent for cases with low expected cell-frequencies, HODGES & LEHMANN, 1970) was used for equivalent comparisons for specific 10-mm size classes.

Mean shell-width growth increments for the tag-recapture period were expressed as annual shell growth rates and were compared between habitats using an ANOVA F-test. Regression analysis was used to estimate the von Bertalanffy growth parameters, L_∞ and K, at sites where both large and small snails were released (RICKER, 1975). The GULLAND & HOLT method (1959) was used to adjust for differences in release time. Confidence intervals were obtained using the routine presented by ABRAHAMSON (1971).

Visceral coils of about 50 snails from each sampling site were preserved in 70% isopropyl alcohol for determination of a gonad index. All snails showing gonadal tissue as determined by visual inspection were considered sexually mature (RANDALL, 1964). A gonad condition index for each specimen was obtained following FEARE (1970). Using a color photo of a cross-section of the visceral coil, the area corresponding to the gonad was expressed as a fraction of the cross-sectional area of the entire visceral coil. Average size at first sexual maturity and size-specific fecundity were compared between habitats using ANOVA F-tests.

RESULTS

Cittarium population densities were significantly correlated with exposure ($F_{(2,13)} = 15.85$, $P < 0.001$). Average densities were highest at EXP sites (6.0 snails/m²) and lowest at SH sites (0.1 snails/m²) (Table 1). Predatory thaid gastropod densities were similarly correlated with exposure ($F_{(2,13)} = 19.84$, $P < 0.001$). Thaids were abundant at EXP sites (0.7 thaids/m²) but virtually absent at the

INT and SH sites examined (Table 1). At EXP sites, *Thais deltoidea* constituted 64% of the 96 thaids seen, while *T. rustica* and *Purpura patula* constituted 24% and 12%, respectively. Sixteen of the 18 thaids (89%) recorded over the course of more than two years at INT and SH sites were *T. deltoidea*, while two (11%) were *P. patula*.

Few population modes were evident in the size-frequency data obtained (Figure 3). Population structures at EXP sites were dominated by small snails (*i.e.*, 15–30 mm shell width). Despite large sample sizes ($n = 174$–446), low abundances of large snails precluded meaningful distinction of more than one population mode. Lack of snails in the larger size classes suggested a high rate of extinction of population modes due to low survival or low growth rates at EXP sites. In contrast, population structures at SH sites were dominated by large snails near the maximum size attained by the species. Indistinct modes at SH sites, due to small sample sizes ($n = 56$–118) and combined with the fact that population modes near L_∞ tend to merge (SAINSBURY, 1982), precluded more detailed analysis of the size-frequency data for survival and growth estimation. The size-frequency data, nevertheless, suggested important differences between habitats in growth or survival.

A total of 19 double-tagged shells were recovered with tags still attached. Of these, 9 had one tag and 10 had two tags. Annual tag shedding was estimated at 55% and did not differ significantly from an estimate obtained in a concurrent study (38%; $n = 43$) using the same tags (DEBROT, 1990). Therefore, the combined estimate of 43%/year was used for the purpose of survival estimation.

Handling survival was not significantly less than 100% for either the large ($\chi^2 = 0.22$, d.f. = 1, $P > 0.5$) or small snails ($\chi^2 = 0.18$, d.f. = 1, $P > 0.5$) released (Table 2). Recovery efficiency for small snails did not differ significantly between habitat types ($\chi^2 = 2.40$, d.f. = 3, $P > 0.50$). By the end of recovery, 96% of the small tagged snails present within 20 m from the points of release at INT and SH sites had been recovered (Figure 4). Recovery efficiency for large snails was estimated at 97%. For both

EXP
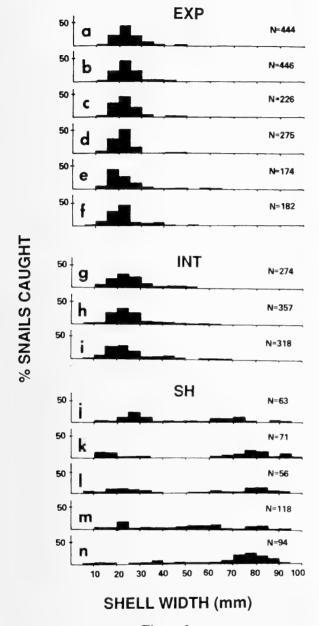
Figure 3

Size-frequency distributions for *Cittarium* collected at the 14 size-frequency collection sites (a–n), grouped by habitat type.

small and large snails, a 100% recovery efficiency was assumed.

Under ideal conditions (*i.e.*, large sample size, no microhabitat selection, and uniform behavior by all members of the population), snail recaptures should decrease with increasing distance from their point of release. In general, recaptures decreased with increasing distance from their point of release (Figure 5). At the EXSS site an estimated 94% of the snails originally released had remained within a 20-m radius from the point of release. At INT sites 67%
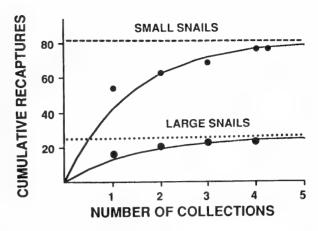
Figure 4

Cumulative number of tagged *Cittarium* recaptured 168–174 days after release versus number of successive collections, for all tag-recapture sites combined. Also shown are the asymptotically estimated numbers of large (· · · · ·) and small (– – –) snails present within 20 m from their points of release.

of the snails had remained within a 20-m radius while at SH sites 85% had. After scaling for differences in total number of recoveries per site, habitat differences in dispersal were significant ($\chi^2 = 15.41$, d.f. = 4, $P < 0.005$).

No dispersal correction factor was calculated for EXP habitat because of few recoveries. However, the two recoveries of small shells made at EXP sites were within 1
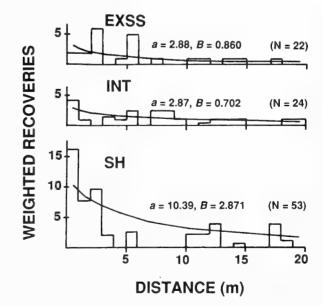
Figure 5

Percentage recoveries of live tagged *Cittarium* as a function of the distance from their points of release, after 168–174 days at large. Fitted curves are of the form $Y = a - B \ln(X)$ where Y is the number of recaptures and X is the distance from the point of release.

Table 3

Tagged-shell releases and recoveries for small *Cittarium* ($\bar{x} = 22.8$ mm) by site, and the corresponding growth and survival estimates. Dashes indicate data not available. Habitat types: exposed (EXP), exposed shallow sloping (EXSS), intermediate (INT), and sheltered (SH).

Habitat type	Site number	Number of snails		Percent recovered	Survival rate (%/year)	Growth rate (mm/year)
		Released	Recovered			
EXP	1	40	2	5	0.7	7.9
	2	40	0	0	<0.2*	—
	3	40	0	0	<0.2*	—
	5	40	0	0	<0.2*	—
				Average:	0.2	7.9
EXSS	4	80	22	27.5	12.7	10.2
INT	6	40	6	15.0	7.2	15.2
	7	40	0	0.0	<0.2*	—
	8	40	2	5.0	0.7	15.2
	9	40	13	32.5	37.5	25.0
				Average:	11.3	18.4
SH	10	40	8	20.0	8.0	22.6
	11	40	4	10.0	1.8	19.4
	12	36	10	27.8	16.1	22.4
	13	40	19	47.5	50.7	31.2
	14	40	12	30.0	19.0	16.9
				Average:	19.1	22.4

* Due to the small number of releases and the fact that fractional recoveries are not possible, the estimates of survival are not continuously distributed. For the cases with zero recoveries, mortality estimates are presented as less than (<) the value that would have been obtained with one recovery. In all such cases, a zero survival value was used in calculating average annual survival for each habitat type.

m from the point of release. The low number of recoveries at EXP sites is not believed to be due to unusually high levels of emigration because searches far beyond 20 m from the point of release yielded no additional recoveries. Survival estimates for EXP sites were, therefore, derived using the dispersal correction factor for INT sites, the most conservative choice.

Survival estimates for small snails differed significantly between the habitats for which multiple estimates were obtained ($P = 0.032$, Kruskal-Wallis test). Lowest average survival was at EXP sites (0.172%/year) where only 2 of the 160 snails released were again recovered. Average survival for small snails was much higher at other sites, averaging 12.7%/year, 11.3%/year, and 19.1%/year for EXSS, INT, and SH sites, respectively (Table 3). For the large snails released, average survival estimates were 6.2%/year at EXP sites and 29.8%/year at SH sites (Table 4) but, with a low number of replicates per habitat type, did not differ significantly ($P > 0.10$, Mann-Whitney U test).

Few large dead shells were collected from EXP sites (Figure 6), mirroring their low abundance in the live snail collections. At both EXP and INT sites, most dead shells were classified as lethally crushed (50% and 42%, respectively). At EXP sites, drilled shells constituted the second-largest fraction, while undamaged shells were the least abundant of the three fractions. In contrast, at INT sites, undamaged shells constituted the second-largest fraction

while drilled shells were the least abundant. Higher fractions of drilled and crushed shells at EXP sites suggested higher predation mortality than at INT sites ($\chi^2 = 20.10$, d.f. $= 2$, $P < 0.005$). However, due to a tendency for larger shells to have a lower incidence of predatory shell damage (Table 5) and due to the difference between habitats in dead-shell size structure, size-specific comparisons were necessary. For snails in the size classes for which comparable samples were obtained (the 30–40 mm and 40–60 mm size classes), P-values of less than 0.06 suggested higher predation mortality in EXP (Table 5).

Average growth rates for small snails were 7.9 mm, 10.2 mm, 18.4 mm, and 22.4 mm/year for EXP, EXSS, INT, and SH sites, respectively (Table 3). Lowest growth rates were in EXP and EXSS habitats, both of which had high snail densities. Small sample sizes precluded statistical comparison of more than two habitats unless estimates from EXP and EXSS habitats were pooled to form a third habitat class. A comparison of growth rates between INT and SH habitats showed no significant differences ($F_{(1,6)} = 1.032$, $P = 0.349$), whereas including a third habitat class (with pooled EXP and EXSS estimates) did result in significant habitat differences ($F_{(2,7)} = 4.918$, $P = 0.046$). For the more limited release of large tagged snails, average growth rates appeared uniformly low among habitat types (Table 4).

Von Bertalanffy growth parameter estimates for EXP

Table 4

Tagged-shell releases and recoveries for large *Cittarium* ($\bar{x}$ = 80.0 mm) by site, and the corresponding growth and survival estimates.

Habitat type	Site number	Number of snails		Percent recovered	Survival rate (%/year)	Growth rate (mm/year)
		Released	Recovered			
EXP	2	17	3	17.6	10.2	4.5
	3	17	2	11.8	4.3	2.6
	5	17	2	11.8	4.3	8.1
				Average:	6.2	5.1
SH	10	17	6	35.3	26.9	3.4
	13	16	8	50.0	56.5	1.9
	14	17	3	17.6	6.1	2.1
				Average:	29.8	2.6

sites also suggested low growth rates compared to SH sites. Using midpoint parameter estimates (Table 6), the age of a 65-mm snail from SH habitat would be about four years, while that of a 65-mm snail from EXP habitat would be about nine years.

Average shell width at first maturity was smallest at EXP sites ($\bar{x}$ = 16.7 mm; range, 14.5–17.8), intermediate at INT sites ($\bar{x}$ = 20.2 mm; range, 18.4–21.4), and largest at SH sites ($\bar{x}$ = 24.2 mm; range, 22.8–27.9), and differed significantly between habitats ($F_{(2,10)}$ = 23.37, P = 0.002). In addition, fecundity levels were consistently lowest at EXP sites (Table 7).

DISCUSSION

The tagging experiment indicated highest rates of mortality for *Cittarium* in EXP habitat. The higher density of molluscan predators and the higher proportion of lethal predatory shell damage, as compared to less exposed habitat, may account for these observations. Growth rates, size at first sexual maturity, and fecundity were the least in EXP habitat. Higher *Cittarium* density may reduce *per capita* food availability in EXP habitat. However, other factors, such as differences in wave stress, air and water temperatures, and floral food value, may also be important factors affecting growth rate, size of maturation, and fecundity.

In contrast, EXSS habitat had high densities of large animals. Growth and survival rates were measured at one EXSS site (site 4). Growth, based on 22 recaptures, was similar to that at other high-density EXP sites and was slow compared to growth rates at SH and INT sites. The survival estimate at the EXSS site was much higher than at EXP sites, suggesting that shallow topography may reduce mortality rates. In particular, dislodgement by waves, which is known to subject snails of wave-exposed habitat

Table 5

Number of *Cittarium* shells in each of three shell-damage categories for shells collected from EXP and INT habitats.

Habitat type	Shell damage category	Shell size (mm)							Percent of total observations
		0–20	21–30	31–40	41–50	51–60	≥61	All sizes	
EXP	Drilled	26	61	41	11	3	1	143	37
	Crushed	14	109	43	15	11	1	193	50
	Undamaged	10	24	9	3	2	5	53	13
	Totals	50	194	93	29	16	7	389	100
INT	Drilled	1	2	3	4	3	9	22	25
	Crushed	0	10	7	11	4	5	37	42
	Undamaged	0	1	11	5	5	7	29	33
	Totals	1	13	21	20	12	21	88	100
	P^*	—	0.952	0.004	0.059	0.194		<0.005	

* P-values compare size-specific importance of predatory mortality (combined crushed and drilled) and nonpredatory mortality (undamaged) between habitats. Fisher-Irwin tests except the comparison for all shell sizes combined. The latter was done using a χ^2 goodness-of-fit test. Dashes indicate test not made.
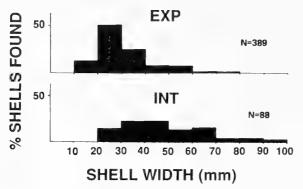
Figure 6

Size frequencies for dead *Cittarium* shells found in EXP and INT habitat types.

to increased predation (UNDERWOOD & DENLEY, 1984; MORAN, 1985), may be less at EXSS sites.

Cittarium size-frequency distributions differed greatly with differences in habitat wave-exposure and topography. A preponderance of small snails was found at EXP sites, where growth rates were low and mortality was high. At SH and INT sites, where growth rates were high and mortality was low, large snails were relatively more abundant.

Large-scale movement of large snails into SH or INT habitat is, in most cases, unlikely because of intervening sandy areas. Because losses due to fishing could also be considered negligible, differences between habitats in terms of survival and growth appear to be the main contributors to the gross differences seen in population structure. Negatively skewed size-frequency distributions, as found in SH habitat, have been described for other reef invertebrates (YAMAGUCHI, 1977). Such distributions may result from size-differential recovery efficiency (APPELDOORN & BALLANTINE, 1983; AULT & DeMARTINI, 1987) or temporal variability in recruitment (FRANK, 1969; UNDERWOOD, 1975) but may also be attributed to animals surviving to near their maximum size. Annual growth increments monotonically decrease at sizes approaching L_∞, and population modes, consequently, tend to merge (SAINSBURY,

Table 6

Von Bertalanffy growth parameter estimates for *Cittarium* with 95% confidence intervals. Parameter estimates are from snails that were at large August 1984–January 1985. K is expressed as an annual rate.

Habitat type	Site number	n	K	L_∞ (mm)
EXP	All sites	9	0.056 ± 0.054	167.94 ± 84.13
SH	10	17	0.291 ± 0.036	84.00 ± 5.95
	13	26	0.659 ± 0.034	81.12 ± 2.18
	14	14	0.369 ± 0.022	88.84 ± 2.83

Table 7

Size-specific average gonad indices (G.I.) and sample sizes for *Cittarium* collected in August 1984 in three habitat types.

	Habitat type						
	EXP		INT		SH		
Size (mm)	G.I.	n	G.I.	n	G.I.	n	P^*
11–20	0.10	4	—	—	—	—	—
21–30	0.11	40	0.30	2	0.16	8	0.468
31–40	0.21	36	0.43	3	0.23	14	0.042
41–50	0.08	31	0.42	8	0.26	11	0.000
51–60	0.10	5	0.29	7	0.33	6	0.056
61–70	0.33	3	0.40	7	0.44	17	0.270
71–80	—	—	0.52	1	0.45	11	—
81–90	—	—	—	—	0.40	7	—

* *P*-values are for statistical comparisons between habitat types. ANOVA *F*-tests. Dashes indicate data not available or test not made.

1982). The latter may explain the negatively skewed size-frequency distributions in this study for two reasons. The first is that all such distributions were from the habitat where survival and growth rates were highest (SH), and where, therefore, the accumulation of old animals was likeliest. The second is that the implied merging of age-class modes occurred near L_∞ and not in the intermediate size classes. Large population modes at intermediate size classes would have suggested that other factors, such as temporal variability in recruitment or survival, were also important factors shaping size structure.

RANDALL (1964) noted that *Cittarium* is generally rare on sheltered coasts. Compared to more exposed habitats, lower population densities in SH habitat could either be from lower levels of settlement or lower levels of subsequent survival. In this study it was found that rates of survival and growth for snails greater than 20 mm were comparatively high in SH habitat. Thus, low densities in SH habitat appear to be caused by factors affecting settlement or the early postlarval stages of the snail.

Factors that may affect settlement include the supply of larvae and settlement preferences. Because SH sites had dramatically lower *Cittarium* population densities in spite of their often close proximity to high snail-density EXP and INT habitats, the low population densities in SH habitat were probably not due to reduced supplies of larvae. Reduced survival of juveniles because of desiccation during low tide may contribute to low densities in SH habitat. In contrast to large snails, those smaller than 10 mm did not appear to migrate to lower intertidal zones during low tide but remained in the upper intertidal zones (DEBROT, 1990). In EXP and EXSS habitats such snails would be wet periodically, but in SH habitat they could experience periods of up to 12 hr without immersion.

Although the cause for lower population densities of

young snails in SH habitat remains unknown, the low densities of conspecifics and predators in such habitat seem to translate into higher growth and survival rates for snails of the size range studied.

ACKNOWLEDGMENTS

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The Diet and Feeding Selectivity of the Chiton *Stenoplax heathiana* Berry, 1946 (Mollusca: Polyplacophora)

by

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Abstract. The chiton *Stenoplax heathiana* Berry, 1946, does not graze randomly but exhibits a high degree of selectivity over the food items ingested. *Plocamium, Gigartina, Polysiphonia, Ulva, Phyllospadix,* and *Rhodymenia* are preferred plant genera. No evidence of "rasping" the substrate for ingestible material was found; instead, this species "nips off" manageable bits of material when foraging.

INTRODUCTION

Stenoplax (Stenoradsia) heathiana Berry, 1946, is a common polyplacophoran mollusk ranging from Bahía Santo Tomas, Baja California, Mexico, to Ft. Bragg, California (PUTMAN, 1980). It is diurnally restricted to the undersides of mid- to lower-intertidal rocks set in sand/mud substrata, nocturnally emerging to forage onto nearby exposed rock surfaces (HEATH, 1899; personal observations).

Although feeding preferences of several California chitons have been described in the literature (BURNETT *et al.,* 1975, and references therein), no treatment has been given *Stenoplax heathiana*. The only mention made of feeding in this species, to the author's knowledge, comes from HEATH (1899) who suggested that *S. heathiana* merely ingests the flora adjacent to the rocks under which it dwells. The suggestion that this species feeds on drift algae is made by RICKETTS *et al.* (1985) and MORRIS *et al.* (1980), but neither source treats species ingested or preferred. The purposes of this study are to define the diet of *S. heathiana* and to determine if this species feeds selectively or randomly.

MATERIALS AND METHODS

Two sites in California were selected, owing to the availability of chitons: Mission Point, Monterey Co. (35°45′N, 121°56′W) and an area about 1.5 km north of the Pigeon Pt. Lighthouse, San Mateo Co. (37°12′N, 121°24′W). Chi-

tons were observed and collected between 2 March 1981 and 27 April 1981, in early morning or afternoon, depending on the time of minus tides. Both habitats are protected outer coasts with extensive intertidal flats of easily overturned rocks set in sand/mud substrata.

Rocks within these areas were temporarily inverted. When one or more individuals of *Stenoplax heathiana* were located, all species of plants and animals within a 0.5-m radius of the chiton(s) were noted. The chiton(s) were collected, tied down in an expanded position onto a wooden lath, and immediately fixed in 10% formalin (ROBB, 1975). Samples of the noted plants were returned to the laboratory for microscopic examination to provide a reference facilitating the identification of ingested food items. Algae were identified using ABBOTT & HOLLENBERG (1976). Vascular plants and animals were identified by the author.

Gut contents of the collected chitons were examined microscopically following ROBB (1975), except that glycerin was used in mounting gut contents onto slides. Genera and/or species in gut contents were noted. Preliminary dissections revealed no substantial difference between intestine and stomach contents; therefore, the stomach and intestine were considered as a whole. Also, preliminary work revealed no identifiable food items located in the midgut glands; consequently, these were not considered further.

The number of chitons within 0.5 m of an available potential food item was noted, along with the number of chitons found to have ingested that food item. Both data were ranked and a Spearman Rank Correlation (SNEDECOR & COCHRAN, 1980) was performed. Also calculated was the percentage of chitons within the area of an avail-

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Table 1

Potential food items, number of chitons within 0.5 m of an available potential food item (Available) and the number of chitons determined to have that food item in the gut (Gut). Total number of chitons collected = 22. Total number of potential food items noted = 29.

Organism	Available	Gut
Gigartina canaliculata	17	11
Corallina chilensis	17	1
Calliarthron cheilosporioides	16	0
Rhodymenia lobata	15	6
Ulva lobata	14	6
Iridaea sp.	9	0
Odonthalia sp.	9	0
Eurystomella bilabiata	9	0
Cryptosiphonia woodi	8	0
Pelvetia fastigiata	8	0
Gigartina sp. (*non canaliculata*)	8	1
Clavelina huntsmani	8	0
Balanus glandula	8	0
Chthamalus fissus	8	0
Spirorbis spirillum	8	0
Fish eggs	8	1
Sponge	8	0
Gastroclonium coulteri	5	0
Rhodomela larix	5	0
Phyllospadix sp.	5	2
Plocamium violacium	4	4
Porphyra sp.	3	0
Ralfsia pacifica	2	0
Polysiphonia sp.	2	1
Pelvetiopsis sp.	2	0
Lithothamnium sp.	1	0
Prionitis lanceolata	1	0
Laurancia sp.	1	0
Egregia sp.	1	0

Table 2

The percentage of chitons within the area of an available food item that were found with the food item in the gut.

Organism	Percent
Plocamium violacium	100
Gigartina canaliculata	65
Polysiphonia sp.	50
Ulva lobata	43
Phyllospadix sp.	40
Rhodymenia lobata	40
Fish eggs	20
Gigartina non canaliculata	13
Corallina chilensis	6

Table 1, ranking available potential food items with those found to be ingested, allowed rejection of the null hypothesis of no difference between the two sets of data at any standard level of significance.

DISCUSSION

From the gut analyses of 22 individuals of *Stenoplax heathiana*, 9 organisms were found to be ingested, with 6 of these selected over other available food items by a high percentage of chitons. This suggests, along with only 9 of the 29 potential food items being ingested, that feeding is not random. Indeed, the Spearman Rank Correlation performed on the data indicates that food item selection, and not random grazing, is taking place.

No encrusting algae such as *Ralfsia* or *Lithothamnium* were noted in gut contents, although these were available as food items. In contrast, clearly identifiable ends of *Gigartina canaliculata* and entire *Corallina* intergenicula were noted, providing evidence that *Stenoplax heathiana* feeds, not by "rasping" at the substrate, but by nipping off ends and bits of algal thalli. This has been observed in other chitons. *Lepidochitona hartwegii* (Carpenter, 1855) (see ROBB, 1975), *Nuttallina californica* (Reeve, 1847) (see NISHI, 1975) and *Mopalia lignosa* (Gould, 1846) (see FULTON, 1975) have each been noted as having large pieces of algae in their guts. Because this mode of feeding appears to be used by *S. heathiana*, the crustose genera would certainly remain untouched. Also, such genera as *Egregia* and *Iridaea*, both available to the animals sampled in this study, would perhaps remain untouched, unlike the more tender, leafy, and thinner algae such as *Rhodymenia* or *Plocamium*.

The presence of animal matter (fish eggs) in the gut of one of the chitons might be viewed as evidence of random grazing or of sampling possible food sources. As the eggs were wholly undigested, however, it seems unlikely that any nutrition could have been provided by these eggs. Hence, I suggest that, although *Stenoplax heathiana* derives most of its food from selective feeding, a certain amount of random grazing or sampling does take place.

able food item determined to have that food item in the gut.

RESULTS

In Table 1 are listed available potential food items. Food items are ranked from highest to lowest availability by the number of chitons noted within 0.5 m of the item, together with the number of chitons in which that food item was found.

One genus of Chlorophyta, *Ulva*, five genera of Rhodophyta, *Corallina, Gigartina, Plocamium, Rhodymenia* and *Polysiphonia*, one genus of vascular plant, *Phyllospadix*, and one form of animal matter, fish eggs, were found in the gut contents. Of these, *Plocamium, Gigartina canaliculata, Polysiphonia, Ulva, Phyllospadix*, and *Rhodymenia* were selected, as shown by the high percentages of chitons found to contain those food items, if available (see Table 2). The Spearman-Rank Correlation run on the data presented in

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Movement Patterns of the Limpet *Lottia asmi* (Middendorff): Networking in California Rocky Intertidal Communities

by

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Abstract. Laboratory observations of marked specimens of *Lottia asmi* (Middendorff, 1847) and *Tegula funebralis* (A. Adams, 1854) over a 27-day period established that movement of limpets between snails was frequent and nocturnal. Limpets changed snails as many as 20 times and as few as 5 times during the study period. Every *T. funebralis* was occupied by 3 or more different limpets, and 5 snails were occupied by 10 or more individuals at different times. Patterns in these data suggest that some *T. funebralis* were ridden more often than others. The number of changes per night ranged between 3 and 11 (mean = 6.67) and time series analysis revealed no periodicity. Cohorts of limpets often occupied the same snail and some of these moved together as units between snails. Radular morphology, behavior, and ecology suggest that *L. asmi* is a more dynamic species than previously thought, and it appears that *L. asmi* is not a snail commensal but rather a carbonate associated species. Carbonate associates are most common in tropical seas where they are associated with corals and other carbonate habitats. In temperate and boreal regions they are commonly associated with coralline algae and other mollusks.

INTRODUCTION

The patellogastropod *Lottia asmi* (Middendorff, 1847) is easy to identify and characterize in California rocky intertidal communities (CARLTON & ROTH, 1975; ABBOTT & HADERLIE, 1980; RICKETTS *et al.*, 1985). The black, high-domed species is best known from the mid intertidal zone where it occurs on the shells of the trochid gastropod *Tegula funebralis* (A. Adams, 1854). Studies of the pair often treat *L. asmi* as a static organism, affixed to the whorls of its motile host. But, observations by GRANT (1933), F. H. TEST (1945), and EIKENBERRY & WICKIZER (1964) have suggested that *L. asmi* has a much more active life style.

The perception of *Lottia asmi* as an innocuous commensal on *Tegula funebralis* was first suspect when GRANT (1933) noted that specimens of *L. asmi* were sometimes found on rock surfaces, and she suggested that these individuals were in the process of transferring between snails. F. H. TEST (1945) published a 1937 study of the movement patterns of *L. asmi* and concluded that limpets rarely spent more than 24 hr on an individual snail. EIKENBERRY & WICKIZER (1964) studied transfer rates in laboratory aquaria and reported that about 75% of the limpets transferred at least once during their 13-hr observation period.

Although both studies were of short duration, and were complicated by either poor field conditions or possible laboratory artifacts, it was evident that *L. asmi* was not uniquely associated with a specific *T. funebralis*.

This paper reports the results of a 27-day study of the movement patterns of *Lottia asmi*. The study was undertaken to annotate the earlier observations of high transfer rates, and to examine longer, time-series movement data for pattern. These data suggest that *L. asmi* is a more dynamic species than previously thought. Also, it appears that *L. asmi* is not a strict snail commensal but rather a carbonate associate, a species that occurs primarily or exclusively on carbonate substrates. Lottiidae associated with carbonate substrates are most common in carbonate-rich tropical seas (CHRISTIAENS, 1975; LINDBERG & VERMEIJ, 1985; LINDBERG, 1988). In temperate and boreal regions they are typically associated with coralline algae (McLEAN, 1966; LINDBERG, 1983, 1988). In the Lottiidae, carbonate obligates form a morphological grade; within subclades the grade may be found in all members or widely scattered among several different groups. Abbreviations used in the text are as follows: LACMIP—Invertebrate Paleontology, Natural History Museum of Los Angeles County, Los Angeles, California; USGSM—U.S. Geological Survey, Menlo Park, California; UCSC—University of California, Santa Cruz, California.
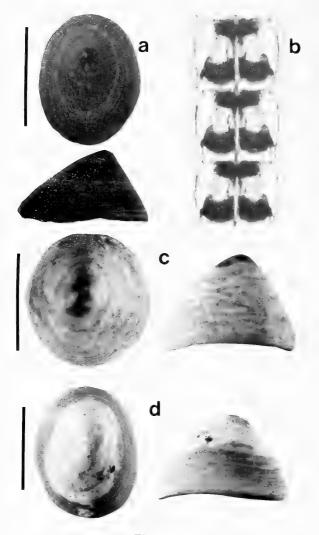
Figure 1

Recent and fossil *Lottia asmi* (Middendorff). Scale bars = 5 mm.
a. Dorsal and lateral views of the shell of *Lottia asmi*; Recent,
Davenport, Santa Cruz County, California. b. Dorsal view of
the radula of *Lottia asmi*. c. Dorsal and lateral views of the shell
of ?*Lottia asmi*; Pliocene, Los Angeles, Los Angeles County, Cal-
ifornia (LACMIP No. 8406). d. Dorsal and lateral views of the
shell of *Lottia asmi*; Middle Pleistocene, San Nicolas Island, Ven-
tura County, California (USGS Loc. No. M21663).

SPECIES, MATERIALS, AND METHODS

Species

Lottia asmi is a small (mean length <10 mm) north-
eastern Pacific lottiid (Figure 1a). It ranges from Cape
Arago, Oregon (about 43°N) to Punta Pequeña, Baja Cal-
ifornia Sur, Mexico (26°N). Although the northern range
limit of this species is often given as Sitka, Alaska (the
supposed type locality), no well documented specimens
have been collected north of Oregon (GRANT, 1933). *Lottia*

asmi is often found on *Tegula funebralis*, but it is also
common on mussels (*Mytilus californianus* and *M. edulis*)
(LINDBERG, 1981) and sometimes on rock (GRANT, 1933;
F. H. TEST, 1945; LINDBERG & PEARSE, in press). The
radular tooth morphology of *L. asmi* is characteristic of
lottiid species associated with carbonate substrates; all three
pairs of outer lateral teeth are blunt and rounded, and the
second pair are markedly broadened (Figure 1b). If *L.
asmi* becomes stranded on rock substrates for several months,
shell color and gross morphology change significantly, and
the resultant shell morphology is similar to other north-
eastern Pacific lottiids (LINDBERG & PEARSE, in press);
movement to these non-carbonate substrates produces no
change in radular morphology.

Tegula funebralis is a mid intertidal species with diurnal
and tidal mediated behavior (see review by ABBOTT &
HADERLIE [1980]). It ranges from Vancouver Island, Brit-
ish Columbia, Canada (50°N) to Isla San Geronimo, Baja
California Norte, Mexico (30°N) (MCLEAN, 1978). Be-
cause *Lottia asmi* extends farther south than *T. funebralis,*
the southernmost specimens of *L. asmi* were probably col-
lected from substrates other than *T. funebralis*.

The first putative specimen of *Lottia asmi* occurs in the
Pliocene Fernando Formation of Los Angeles, California
(Figure 1c) (>1.6 Ma). It differs from living specimens
in having a more circular aperture. When viewed in profile,
however, the aperture has a distinctive sigmodial shape
that is shared with Recent specimens. The next record is
from a Middle Pleistocene terrace on San Nicolas Island,
Ventura County, California (Figure 1d) (VEDDER &
NORRIS, 1963), about 0.6 Ma (MUHS, 1985). Subsequent
records are lacking until the oxygen-isotope substage 5e
of the last interglacial (Sangamon, approximately 0.120
Ma) (MUHS, 1985), and these records include many lo-
calities in southern California and Baja California Norte,
Mexico (Lindberg, unpublished data). *Tegula funebralis*
first appears in the upper Pico Formation (Early Pleis-
tocene) near Ventura, California (GRANT & GALE, 1931),
about 1.1 Ma (LAJOIE *et al.,* 1982).

Materials and Methods

Seventeen specimens of *Tegula funebralis,* each with a
single specimen of *Lottia asmi* aboard, were collected at
Pigeon Pt., San Mateo County, California on 14 February
1981. The limpets were carefully removed from the snails,
and both were marked with small (approximately 2 mm
× 2 mm), numbered squares of waterproof, plastic paper
affixed to the apex of the shells with a cyanoacrylate-based
glue. After measuring the limpets and snails to the nearest
0.1 mm with vernier calipers, a single limpet was randomly
selected and placed on each *T. funebralis.* The trochids
were then placed on concrete cinder blocks in an outdoor
fiberglass tank equipped with a drip seawater system at
the Long Marine Laboratory, UCSC. The drip seawater
system was constructed of polyvinyl chloride (PVC) plastic
pipe and fittings. Holes were drilled at intervals along the

Matrix A

T. funebralis / *L. asmi*

L. asmi \ T. funebralis	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	RK	A	B	C
1	1		1		3	1		3	1	1	1	2	2		1		2	1	12	19	20
2	3	1			1				1				1					2	5	7	6
3			1		3	1		1	1							1		1	6	8	7
4			1					1	2	1		1	2	1				2	7	9	9
5	1	1	1		1		1	1	1							1	1		9	9	
6			1		2	1							3		1		2		6	10	
7		3		1					1		1	1	1		3	1	1		9	13	
8	1	3	1	1	2				1				1				3		8	13	
9		1						1	2	1		1		1	2				7	9	
10	1	1	2			1	2	1	1			1		1	1		2		11	14	
11		1						1	3	2		3	1		2				7	13	
12		1			1	1			2			1			1	3	2		8	12	
13		3	1		2	1		2		1			1	1	2		3		10	17	
14	1	2	2		1			2				2			1		1		8	12	
15				1							1		1				2		4	5	
16		2	1	1	1				1			1	1		1	1	1		10	11	
A	6	10	10	5	9	6	3	9	11	6	3	9	8	5	10	6	11	4			
B	8	18	12	5	14	8	4	13	16	7	3	13	11	6	14	9	20	6			

Matrix B

T. funebralis / *L. asmi*

L. asmi \ T. funebralis	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	RK	D
1	1		1		3	1		3	2	2	2	3	4		1		3	1	27
2	10	1			3				1				1					10	26
3			1		10	1		3	3						4			5	27
4			1					3	2	1		1		8	1			10	27
5	2	2	6		1		2	1	1							10	1		26
6			8		3	2						3		1			8		25
7		6		3				1		2	6	1		4	2		1		26
8	2	6	6	1	2			3				1					6		27
9		2						1	12	4		1		4	2				26
10	3	1	7			1	2	1	3			3		3	1		2		27
11			1					2	10	4		4	2			4			27
12		3			1	1			2			1			1	11	5		25
13		5	1		5	1		2		1			1	1	2		8		27
14	3	9	2		1			3				3			3		2		26
15										19		1					6		27
16		6	1	1	1			2				1	1		2	10	1		26
C	21	41	34	7	20	16	5	19	39	15	23	23	14	17	18	41	43	26	

Figure 2

Data summaries. Matrix A (upper). The value in each cell of the large matrix is the number of times a numbered limpet (*Lottia asmi*) was found on each numbered snail (*Tegula funebralis*). The entries in column A are the total number of different snails ridden by each limpet and those in column B are the total number of transfers between snails by each limpet. Row A provides the number of different limpets found on each snail or on cinder block (RK); row B provides the total number of times a snail had limpets aboard or limpets were on RK. Data for time spent off *Tegula funebralis* are listed under RK (on cinder blocks) and column C lists the total number of transfers between all substrates (snails and rock). Matrix B (lower). The value in each cell of the large matrix is the total number of days a numbered limpet spent on each snail. Column D provides the number of observations of each limpet (includes RK occurrences; a complete data set = 27 observations). Row C provides total "limpet days" for each snail or RK.

Figure 3

Frequency distributions of the number of unique associations formed by individual *Lottra asmi* with each *Tegula funebralis* (upper) and *vice versa* (lower). The figure to the right of each histogram plot presents a graphic test for normality of these data using rankits. In the case of *L. asmi* the deviation of the rankit values from a straight line suggests a normal or slightly leptokurtic frequency distribution; for *T. funebralis* the rankit values indicate bimodality in the data (see SOKAL & ROHLF, 1981:123).

pipe lengths from which seawater would drip down on the cinder blocks. The cinder blocks were set in sand and the runoff from the blocks percolated through the sand and exited the tank through a drain. Limpet position was recorded twice daily, once in the early morning and once in the late afternoon for 27 days (16 February to 15 March 1981). Limpet no. 17 was found dead on 17 February and therefore the results report the movements of only 16 limpets.

The raw data were analyzed by constructing two preliminary matrices. The first listed each limpet's position in the tank (*Tegula funebralis* number or rock) by date, while the second contained limpet numbers on *T. funebralis* by date. These matrices were used to produce two addi-

tional matrices that summarize the raw data. The first matrix reports the number of times a particular limpet was found on each *T. funebralis* (Figure 2, matrix A), while the second matrix gives the number of days a particular limpet was associated with a specific *T. funebralis* (Figure 2, matrix B). Selected patterns from these data matrices were further quantified, graphed, and tested for statistical significance (SPSS, INC., 1986). The mean number of days a particular limpet and snail were associated was calculated by dividing each cell in Figure 2, matrix B, by its corresponding cell in Figure 2, matrix A. The higher this value, the fewer the moves and the longer the visits.

The lateral surface area of the *Tegula funebralis* shells was estimated by modeling the shells as cones as follows:

lateral surface area $= \pi rs$

where $r =$ the radius of the shell base and $s =$ the slant height of the shell. The value of s was obtained by solving for the hypotenuse of a right triangle as follows:

$$s^2 = r^2 + b^2$$

where $b =$ shell height. The surface area of the shell base was not included in the estimate because this region was seldom used by *Lottia asmi*.
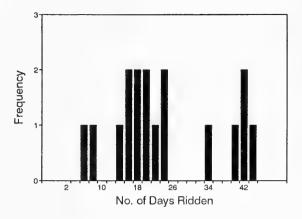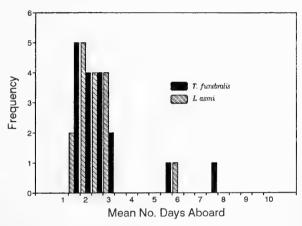
RESULTS

Lottia asmi moved between specimens of *Tegula funebralis* often during the study period. Limpets changed substrates as many as 20 times and as few as 5 times (Figure 2, matrix A). Every *T. funebralis* was occupied by 3 or more different limpets during the study period, and 5 snails were occupied by 10 or more (Figure 2, matrix A). The number of unique associations for limpets appears normally distributed, while the distribution for snails has a distinctly bimodal distribution (Figure 3). This latter distribution suggests that some *T. funebralis* were more "popular" than others with the limpets. The number of limpet days for each *T. funebralis* ranged between 5 and 43 (Figure 2, matrix B), and also shows a possibly bimodal trend (Figure 4). Whether these patterns resulted from the limpets' or snails' behavior is not known.

For *Lottia asmi* the ratio of days aboard to times visited varied between 1.4 and 6.0 (mean = 2.4). For *Tegula funebralis* the ratio varied between 1.3 and 7.7 (mean = 2.4). Both distributions are skewed to the left (Figure 5).

The twice-daily observations of the positions of numbered limpets and snails demonstrated that movement occurred at night; associations recorded during the morning were always still in place in the late afternoon. Although the experimental setting removed *Tegula funebralis* from tidal and other mass water movements, the drip system kept the substrate constantly wet, thus allowing the snails to move and graze at anytime. However, *Tegula funebralis* remained aggregated at the base and within the holes of the cinder blocks during the day. The minimum number of changes per night ranged between 3 and 11 (mean = 6.67) (Figure 6). Time-series analysis of the number of changes per night revealed that the series was stationary, but heteroscedastic; examination of the autocorrelation functions revealed no periodicity in the time series.

More than one limpet often occurred on each *Tegula funebralis*. Groups of 2 *Lottia asmi* formed 36 times on 14 of the *T. funebralis*, groups of 3 formed 10 times on 7 of the snails, and 4 snails had groups of 4 once during the study period (Table 1). Groups of two moved together as a unit 9 times, while groups of 3 or more never moved as units. The longest a group of 2 remained together was 9 days, for a group of 3 it was 10 days, and for a group of 4 it was 5 days. The longest period a *T. funebralis* went without a rider was 14 days and about 40% of the snails were bare at any given time (Table 1).

Explanation of Figures 4 and 5

Figure 4 (upper). Frequency distribution of the total number of days each *Tegula funebralis* had limpets (*Lottia asmi*) aboard during the 27-day study period. Values greater than 27 result when more than one limpet was present on the snail on the same day. Figure 5 (lower). Frequency distributions of the mean number of days each *L. asmi* spent aboard individual *T. funebralis* and the mean number of days each *T. funebralis* was ridden by individual *L. asmi*.

Four *Lottia asmi* moved onto the cinder blocks during the study period (Figure 2). Two of these limpets spent almost one-third of the study period on the cinder blocks (Figure 2, matrix B). The data for cinder block specimens most likely represent minimum values. Because the snails were not handled during the study, not all the specimens of *L. asmi* were accounted for each day (Figure 2, matrix B, column D) and missing specimens may have been overlooked among the clumps of algae on the cinder blocks. If the missing data represent additional cinder block specimens, then 11 *L. asmi* would have been on cinder blocks at sometime during the study for a total of 35 limpet-days (Figure 2, matrix A).

Regressions of total cohort days (Figure 7) and total limpet days (Figure 8) on shell surface area suggest that there is a positive relationship between these pairs of variables. In both cases, however, these trends are driven by
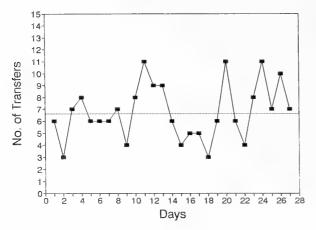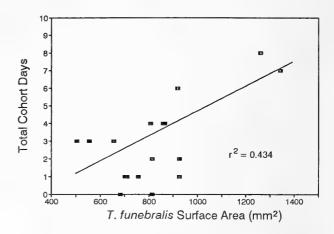
Figure 6

Time-series plot showing the number of transfers, between *Tegula funebralis* by *Lottia asmi*, per day during the 27-day study period. The dashed line indicates the mean number of transfers per night.
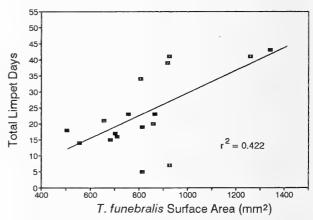
two specimens with shell surface areas in excess of 1000 mm². If these two specimens are removed from the analysis, the patterns appear substantially less linear.

DISCUSSION

Transfer rates in this study are lower than those reported by F. H. TEST (1945) and EIKENBERRY & WICKIZER (1964). F. H. TEST (1945) reported that *Lottia asmi* transferred at least once every 24 hr and EIKENBERRY & WICKIZER (1964) reported that 75% of their laboratory populations transferred overnight. In this study about 40% of the population transferred between *Tegula funebralis* nightly, and the minimum average transfer rate was about 6.7 transfers per day (Figure 6). F. H. TEST (1945) states that his field observations were complicated by tag loss and this may have contributed to his higher rate. EIKENBERRY & WICKIZER'S (1964) study was done in laboratory bowls and aquaria and these conditions may have influenced snail and limpet movement.

The absence of periodicity in the time-series analysis suggests that limpet movement patterns are not correlated with tidal or lunar cycles, and rather are random. The possibility that certain *Tegula funebralis* are occupied more often by limpets than others is suggested by several trends (Figures 2, 3, 4; Table 1), but two different patterns of ridership produce these more popular snails. Some individuals (*e.g.*, snails 2, 3, 9, 17) were ridden by many different limpets (>10), often occurring simultaneously on the snail (Table 1), that remained on average for more than 3 days (Figure 2, matrix B). In other cases (snails 1, 11, 16) individuals were ridden a few times (<6), seldom by cohorts (Table 1), but had limpets that remained for 10 or more days. In summary, examination of the movement data revealed no unequivocal, statistically significant patterns.

Explanation of Figures 7 and 8

Figure 7 (upper). Scatterplot of the total number of days cohorts of *Lottia asmi* (≥2 limpets) spent on individual *Tegula funebralis* regressed against the lateral surface area of the snail's shell. Figure 8 (lower). Scatterplot of the total number of days each *T. funebralis* had limpets aboard during the 27-day study period (Figure 4) regressed against the lateral surface area of the snail's shell.

The behaviors of *Lottia asmi* and *Tegula funebralis* are ultimately responsible for the patterns present in the data. *Lottia asmi* can chemically locate *T. funebralis* both in field and laboratory settings (F. H. TEST [1945] and ALLEMAN [1968], respectively). Once a snail is located and boarded the snail's behavior will play a large role in determining limpet transfer rates. *Tegula funebralis* forms aggregations in different tidal and light conditions. Aggregations occur during daytime low tides and during nighttime high tides (WARA & WRIGHT, 1964). When submerged during daylight high tides, the snails are active and scattered, but if water movement becomes too extreme, the snails will seek shelter (KOSIN, 1964; OVERHOLSER, 1964; ABBOTT & HADERLIE, 1980). During nighttime low tides snails are also active and dispersed (Lindberg, personal observations).

Table 1

Distribution of cohorts of *Lottia asmi* on *Tegula funebralis* and time periods unoccupied.

T. funebralis no.	Cohort size			Days bare
	2	3	4	
1	2	1	0	12
2	5	2	1	4
3	2	1	1	11
4	1	0	0	20
5	4	0	0	13
6	1	0	0	11
7	0	0	0	22
8	2	0	0	9
9	3	2	1	6
10	0	0	0	12
11	1	0	0	4
12	4	0	0	10
13	3	0	0	16
14	1	0	0	13
15	2	1	0	12
16	1	1	0	6
17	4	2	1	2
Totals	36	10	4	183

The aggregation behaviors of *Tegula funebralis* facilitate *Lottia asmi* transfers between snails. Therefore, once attached to the *T. funebralis* population, the snails' aggregation behavior guarantees that *L. asmi* can locate other suitable patches of microhabitat (*i.e.*, other *T. funebralis*) (also see Phillips in RICKETTS *et al.*, 1985).

The impetus for transfers likely results from the limited food reserves of the *Tegula funebralis* shell. EIKENBERRY & WICKIZER (1964) found that *Lottia asmi* ate between 2.7% and 7.0% of the algae on the shell of *T. funebralis* per hour. At the average grazing rate (4.7% shell algae eaten/hr) a limpet would denude a *T. funebralis* shell in 21.4 hr, and grazing is often so intense that the entire exterior surface of the *T. funebralis* shell become grooved (HICKMAN & MORRIS, 1985).

Riding the *Tegula funebralis* network is also a very efficient way for *Lottia asmi* to move about the mid intertidal zone. *Lottia asmi* moves at 12.8 mm/min (F. H. TEST, 1945) while *T. funebralis* is almost 4 times faster at 42 mm/min (ABBOTT & HADERLIE, 1980). *Lottia asmi* does not appear to ride the even faster hermit crab network. The rarity of *L. asmi* on dead *T. funebralis* shells occupied by *Pagurus* spp. (F. H. TEST, 1945; EIKENBERRY & WICKIZER, 1964) probably results from the crabs' aggressive intraspecific behavior (RICKETTS *et al.*, 1985) that precludes hermit crab aggregations, and therefore opportunities for the limpets to transfer.

Based on the first occurrences of *Lottia asmi* and *Tegula funebralis* in the fossil record of southern California, *L. asmi* may have been riding the *T. funebralis* network for over 1.0 million years. The gross morphology of the putative *L. asmi* from the Fernando Formation (Figure 1c) suggests an association with a *T. funebralis*-like snail had already been established by the Late Pliocene (more than 0.5 million years *before* the first appearance of *T. funebralis*). Although fossil specimens of *T. funebralis* date only from the Early Pleistocene (about 1.1 Ma), several *Tegula* spp. are common in Middle and Late Pliocene deposits in southern California (GRANT & GALE, 1931; L. G. Hertlein, unpublished MS), and could have provided substrates for Pliocene *L. asmi*. Non-epizoic fossil specimens of *L. asmi* are not known, but undoubtedly exist and likely have been misidentified (see LINDBERG & PEARSE, in press). Alternatively, the Fernando specimen may not be *L. asmi*; several other lottiid species are known to occur on trochid gastropods (BREWER, 1975; LINDBERG, 1981). The first unequivocal specimen of *L. asmi* (Figure 1d) appears in the Middle Pleistocene of San Nicolas Island off southern California (about 0.6 Ma or about 0.5 million years *after* the first appearance of *T. funebralis*).

Reappraisal of *L. asmi* as a Carbonate Obligate

The association of *Lottia asmi* with *Tegula funebralis*, and the morphological consequences for the limpet, have made *L. asmi* easy to recognize and characterize. A. R. G.

Table 2

Temperate northeastern Pacific carbonate associate species.

Taxon	Habitat	Latitudinal distribution
Acmaea mitra Rathke, 1833	Encrusting coralline algae	52°N to 30°N
Erginus sybaritica (Dall, 1871)	Encrusting coralline algae	60°N to 57°N
Erginus apicina (Dall, 1879)	Encrusting coralline algae	56°N to 53°N
Erginus moskalevi (Golikov & Kussakin, 1972)	Encrusting coralline algae	55°N to 53°N
Niveotectura conica (Gould, 1846)*	Encrusting coralline algae	55°N to 25°N
Lottia asmi (Middendorff, 1847)	Other mollusks	43°N to 26°N
Lottia triangularis (Carpenter, 1864)	Branching and encursting coralline algae	59°N to 34°N
Lottia sp. (undescribed)	Encrusting coralline algae	53°N to 38°N
Tectura rosacea (Carpenter, 1864)	Encrusting coralline algae	55°N to 29°N

* Although formerly regarded as junior synonym of *Acmaea mitra* (Rathke, 1833), the shell structure of the holotype of *Patella conica* Gould, 1846, clearly indicates that this species name is a senior synonym of *Scurria mitra* var. *funiculata* Carpenter, 1864.

TEST (1945:17) suggested that *L. asmi* was derived from *Lottia pelta* (Rathke, 1833) by "ecologic segregation and selection." Although she provided no characters to support the supposed relationship, Test proposed that dwarf specimens of *L. pelta* became associated with *T. funebralis* and subsequently became isolated from *L. pelta* populations. Test was unaware that many characters that she thought inviolable and extreme variants of the ancestral species were phenotypic expressions of living on *T. funebralis*. For example, the gross shell morphology (small size, dome-shape, *etc.*) and dark coloration only occur when the limpet is living on *T. funebralis* (LINDBERG & PEARSE, in press). Specimens of *L. asmi* from rock substrates are similar to most other eastern Pacific *Lottia* species, and the modification of the radula for carbonate feeding masks its ancestry. *Lottia asmi* was included in WALKER's (1968) study of the jaw, digestive system, and coelomic derivatives of several central California *Lottia* species, but the characters treated do little to resolve the ancestry of *L. asmi*. The general jaw morphology of *L. asmi* is substantially different from the other *Lottia* species examined by Walker. Salivary gland morphology grouped *L. asmi* with *L. pelta* and "*Collisella*" *scabra* (Gould, 1846), but *L. asmi* was the only species examined in which the posterior glands were very small and light green in color. Moreover, in *L. asmi* the hindgut was substantially longer than in the other species. Whether these characters are related to the carbonate feeding strategy of this species is not known.

The common occurrence of *Lottia asmi* on the shells of other mollusks, notably *Tegula funebralis*, *Mytilus edulis*, and *M. californianus,* and its rareness on non-carbonate substrates, combined with the morphology of the radular lateral teeth, suggest that *L. asmi* is a carbonate associate. Species that occur primarily or exclusively on carbonate substrates are broadly distributed in the Patellogastropoda (LINDBERG, 1988; Lindberg & Padilla, unpublished data). Carbonates associates may be present in an entire subclade (*e.g.*, *Patelloida profunda* group [CHRISTIAENS, 1975; LINDBERG & VERMEIJ, 1985], *Erginus* spp. [LINDBERG, 1983; LINDBERG & MARINCOVICH, 1988]) or randomly scattered within a clade and clearly convergent (LINDBERG, 1988; Lindberg & Padilla, unpublished data). The shells of these species are typically colored by the pigments present in the carbonate substrates, and the radulae have broad, rounded second lateral teeth and the third lateral teeth also may be enlarged.

Carbonate substrates used by these limpets include both plants and animals. Epiphytic species are found on encrusting and branching calcareous algae, while epizoic species are most often found on the shells of other mollusks (*e.g.*, mussels, oysters, chitons) or on the skeletons of dead corals. The earliest record of this grade is from the Early Cretaceous of England where *Patelloida tenuistriata* (Michelin, 1838) lived on dead ammonite shells (AKPAN *et al.,* 1982). On the basis of the morphology of the rasp marks left on ammonite shell, its radular morphology was identical with that of living carbonate associated species (AKPAN

et al., 1982). Recently, ZINSMEISTER (1990) has reported an "acmaeid" limpet associated with a bivalve mollusk from the Late Cretaceous of Antarctica.

Extant carbonate associates living on mollusks are common in both tropical and temperate settings. In the Caribbean, *Lottia leucopleura* (Gmelin, 1791) often occurs on the trochid gastropod *Cittarium picta* (Linné, 1758) (PILSBRY, 1891). In Chile, *Scurria parasitica* (Orbigny, 1841) is so named because it lives on the shells of the gastropods *Scurria viridula* (Lamarck, 1819) and *Fissurella* spp. and on the chitons *Acanthopleura echinata* (Barnes, 1823) and *Enoplochiton niger* (Barnes, 1823) (MARINCOVICH, 1973). In tropical Australia, *Patelloida bellatula* (Iredale, 1929) occurs on *Lithothamnion,* coral, beach rock, and dead shells, and *Patelloida mimula* (Iredale, 1924) lives on oysters (*Saccostrea*) in tropical and temperate estuaries (PONDER & CREESE, 1980). In temperate Australia, *Patelloida mufria* (Hedley, 1915) and *Patelloida nigrosulcata* (Reeve, 1855) occur primarily on other gastropods (PONDER & CREESE, 1980). Members of the *Patelloida profunda* group are also present in Australia, and include *P. profunda calamus* (Crosse & Fischer, 1864) and *P. profunda ivani* (Christiaens, 1975). Northeastern Pacific carbonate associates are listed in Table 2.

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Sexual Dimorphism in *Pomacea canaliculata* (Gastropoda: Ampullariidae)[1]

by

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Abstract. The Argentine apple snail, *Pomacea canaliculata* (Lamarck, 1822), shows sexual dimorphism in the shape of the shell aperture and the operculum, whose relative widths are significantly different between sexes. The shape of these structures is therefore a reliable means of externally sexing the snails. Males also bear a heavier shell than females. Consideration of sexual dimorphism will improve the predictive curves relating linear measurements and biomass. A test for sexual shell dimorphism would also enhance taxonomic understanding of some conchological species.

INTRODUCTION

While studying *Pomacea canaliculata* (Lamarck, 1822) a shell dimorphism involving the shape of the aperture and the operculum was observed. A similar observation was made by HALE (1964) and DEMIAN & IBRAHIM (1972) for the planorboid ampullariid *Marisa cornuarietis* (L.). The females of both species have a narrow aperture compared with the more rounded one of the males. To an experienced eye this dimorphism permits routine external sexing of most specimens, with a high degree of reliability. Though some males show a narrower aperture, expanded peristomes are infrequent in females. In this paper a preliminary analysis of the dimorphic condition is presented and its ecological and taxonomic derivations are discussed.

MATERIALS AND METHODS

Thirty-four live individuals of *Pomacea canaliculata*, collected at Palermo Park (Buenos Aires city, Argentina) in February 1987, were used to test a hypothesis of sex related differences. All specimens were within the size range of mature adults (MARTIN, 1986).

Shells and opercula were measured with a Vernier caliper to the nearest 0.01 mm, and the animals were then dissected to ascertain their sex. Figure 1 shows the measurements taken. The aperture length was measured on its largest axis (*i.e.,* obliquely to the columellar axis) and the aperture width was measured perpendicular to the length. This way of measuring fits the operculum proportions better than the custom of using the aperture length parameter parallel to the largest axis of the shell.

The shells were weighed to the nearest 0.01 g. For the analysis of shell weight the largest female and the smallest male were omitted from the calculations in order to study the same size range for both sexes.

RESULTS

Figure 2 shows two examples in which the relative width of the aperture illustrates the mentioned sexual dimorphism. The perimeter of the operculum is smooth and generally coincides with the shape of the aperture in the females. In the males it is often wider, showing a sinuous surface and an irregular outer edge.

Table 1 summarizes the characteristics of the studied material. There is no significant difference between the shell width-length ratio of males and females ($t = 0.297$, $P > 0.70$, d.f. $= 32$) or between the aperture length-shell width ratio ($t = 0.503$, $P > 0.60$). The length of the body whorl is almost equal to the shell width and is not a dimorphic character ($t = 1.300$, $P > 0.20$). The width-length ratio of the operculum was compared to that of the aperture using a paired t test, which gave a non-significant value of 0.648 ($P > 0.40$). The analysis could therefore be carried out equally well on the peristome or on the operculum.

[2] Researcher of the Comisión de Investigaciones Científicas de la Provincia de Buenos Aires, Argentina.
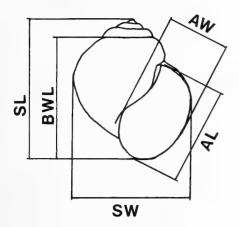
Figure 1

Measurements of *Pomacea canaliculata* shells. AL, aperture length; AW, aperture width; BWL, body whorl length; SL, shell length; SW, shell width.

Figure 3

Scatter plot of operculum width/operculum length versus shell width in the two sexes of *Pomacea canaliculata.*

The operculum width-length ratio is not significantly correlated to shell size (width) within this range, in either sex: $r = -0.1329$ for the females; $r = -0.2790$ for the males. The operculum ratio shows little overlap between sexes (Figure 3), a critical level of discrimination being near 0.72. The comparison of the mean operculum ratios yielded a highly significant difference between sexes: $t = 10.45$, $P < 0.001$.

Figure 4 shows the regression lines of shell weight (*SWe*) as a function of shell width (*SW*):

Males:	$SWe = 0.27136SW - 5.72112$
Females:	$SWe = 0.26807SW - 6.71721$

The analysis of covariance of the regressions over sexes indicated a significant difference ($F = 7.694$, $P < 0.002$,

d.f. = 2 and 28). The hypothesis of equality of the slopes was not rejected ($F = 0.0015$, $P > 0.96$), and it is thus the intercepts which are the source of the dissimilarity.

The males have a heavier shell than the females, and the difference in shell weight-shell width ratio between the sexes is highly significant: $t = 3.64$, $P < 0.01$, d.f. = 30).

DISCUSSION
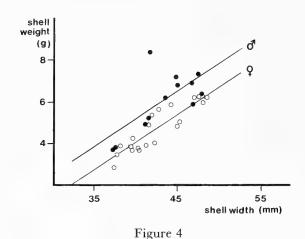
Pomacea canaliculata is the second ampullariid species in which sex dimorphism has been reported. HALE (1964) described a similar feature in a Puerto Rican population of *Marisa cornuarietis* (L.), illustrating it by means of a scatter plot. She said that the difference was "much less evident" in a Florida population of the same species, but

Figure 2

A female (left) and a male (right) specimen of *Pomacea canaliculata* illustrating sexual dimorphism in the relative width of the aperture.

Figure 4

Regression lines of shell weight as a function of shell width in *Pomacea canaliculata*.

no numerical information was included to assess level of significance. DEMIAN & IBRAHIM (1972) carried out a more extensive study on the same species. They also found that shell aperture provides the most significant sex-related differences, and detected less obvious signs of dimorphism on other shell and pigmentation characters. We found sex-related expanded apertures in *P. canaliculata* populations from different localities.

The opercular ratio for some *Pomacea canaliculata* from Brazil is 61.1 to 79.4, with a general mean of 67.36 ± 3.90 ($n = 87$) (GUEDES *et al.*, 1981). These values are not different from those presented in Table 1 ($t = 1.08$, $P > 0.2$, d.f. = 119), suggesting a high degree of similarity between the Argentinian and Brazilian populations.

The expansion of the male peristome is probably related to the great development of the penial complex, which gives rise to an appreciable swelling under the right side of the mantle edge in many ampullariids (HYLTON SCOTT, 1957; ANDREWS, 1964). Thus, the dimorphic condition may be common among other Neotropical apple snails.

When determining sex on the basis of empty shells of *Pomacea canaliculata*, it is useful to consider the aperture length obliquely, on its greatest axis. The more customary vertical measurement would obscure the differences between sexes, which are clear in the operculum proportions.

GUEDES *et al.* (1981) studied the correlations among linear parameters and the weight of the shell and of the soft parts in *Pomacea canaliculata*, and found that the weakest correlations were those involving shell weight. Because they did not separate males from females, this low correlation could be due in part to the dimorphic condition of the shell weight. The reproductive effort in this species is higher than in other gastropods in temperate waters (Estebenet & Cazzaniga, unpublished data), and the relative weakness of the female shell may therefore be related to the expenditure of calcium to build eggshells.

There are several conceivable ecological and taxonomic consequences of shell dimorphism.

Ecology: *Pomacea canaliculata* and related snails are widespread in the Neotropical Region (CAZZANIGA, 1987). They constitute the main diet of some birds (SNYDER & KALE, 1983; BOURNE, 1983), and are eaten by caimans (DIEFENBACH, 1979), turtles, and other native vertebrates (RUSSELL, 1972). By assessing their biomass on the basis of linear shell measurements it is possible both to evaluate the energy budget of live populations without employing destructive techniques and to estimate the biomass con-

Table 1

Shell measurements and weights of the studied specimens of *Pomacea canaliculata* (Lamarck, 1822) from La Plata.

	Females ($n = 21$)			Males ($n = 13$)		
	Min	Max	Mean ± SD	Min	Max	Mean ± SD
Shell length (SL)	42.8	61.7	48.21 ± 4.53	39.0	53.8	47.85 ± 5.00
Shell width (SW)	37.7	57.8	43.13 ± 4.79	33.2	48.0	42.53 ± 4.44
Body whorl length (BWL)	36.7	59.5	42.43 ± 5.04	34.1	47.8	42.45 ± 4.21
Aperture length (AL)	31.3	49.5	35.79 ± 4.17	28.4	40.0	35.08 ± 3.37
Aperture width (AW)	21.3	33.9	24.47 ± 2.88	20.5	29.0	25.65 ± 2.72
Operculum length (OL)	26.2	44.0	30.95 ± 3.87	26.1	35.3	30.97 ± 2.96
Operculum width (OW)	17.0	29.2	20.40 ± 3.27	18.8	26.0	22.41 ± 2.22
Shell weight† (SWe)	2.83	6.97	4.65 ± 1.04	3.67	8.38	6.03 ± 1.38
100 SW/SL	82.68	97.91	89.40 ± 3.71	80.16	96.47	88.98 ± 4.48
100 BWL/SW	92.16	103.66	98.38 ± 3.37	94.87	106.55	99.93 ± 3.38
100 AL/SW	78.53	87.02	82.97 ± 2.65	77.38	88.35	82.62 ± 3.09
100 AW/AL	64.52	73.99	68.40 ± 2.47	70.14	77.60	72.99 ± 2.16
100 OW/OL‡	63.64	72.22	66.78 ± 2.35	70.59	77.78	75.35 ± 2.05
100 SWe/SW†	9.13	13.34	10.86 ± 1.78	9.84	20.24	13.83 ± 2.86

† Calculated from 20 females and 12 males.

‡ General mean ($n = 34$): 68.30 ± 5.14.

sumed by predators who leave the empty shells. However, females have heavier soft parts than males (GUEDES *et al.*, 1981). Because the intercepts of the biomass regressions of both sexes are significantly different, BOURNE & BERLIN (1982) stated that "an overall equation, although possibly still useable, would show a consistent bias in prediction depending on the sex of the individual." We suggest that it is possible to identify reliably the sex of each specimen and to use differentiated regression equations to predict the biomass.

GUEDES *et al.* (1981) defined an operculum product (length × width) that they used as an independent variable in a regression on living weight. This parameter seems to be inadequate, considering the observed sexual differences in operculum width. A female will have a lower operculum product but a greater biomass than a male of the same operculum length, and the dispersion from an overall regression curve will therefore be greater.

The identification of sex in empty shells should make it possible to establish whether predation by kites and limpkins exerts the same pressure on both sexes, since random capture on the normally 1:1 sex ratio of *Pomacea* populations (MARTIN, 1984)[3] would yield an equivalent ratio in the mounds of shells at feeding sites. Should this not be the case, then differential activities in either sex— as have already been found in other prosobranchs (RIBI & ARTER, 1986)—and/or other factors affecting their capturability should be included in the analysis.

Taxonomy: Some detailed studies on the anatomy of several species are available, but most ampullariids have still not been well-defined (PAIN, 1972). Though shells are variable, the form of the aperture has frequently been used as a diagnostic character. At least in two genera, some taxonomic doubts can be dispelled through an analysis of sexual dimorphism in the shell.

PILSBRY (1933) described *Marisa planogyra,* from Brazil, as differing from the type species, *M. cornuarietis,* based on, among other things, the fact that "the last whorl and the aperture are less expanded in the upper and basal parts" in the former. Taking into account the results of HALE (1964) and DEMIAN & IBRAHIM (1972), as well as our present findings, this diagnostic characteristic of *M. planogyra* could correspond to female shells. OLAZARRI (1977) suggested that the two species could be synonyms.

Also, a significant variation in the aperture was mentioned in the supraspecies *Pomacea canaliculata* (*sensu* CAZZANIGA, 1987). For example, *P. levior* (Sowerby, 1909) was differentiated by its expanded outer lip. GEIJSKES & PAIN (1957), studying *P. dolioides* (Reeve, 1854) from Surinam, found that "in some specimens the peristome is wider than normally as in those described by him [Vernhout, 1914] as *levior*." A similar observation was also made

by PAIN (1960) with regard to *P. lineata* (Spix *in* Wagner, 1827) from Brazil, in whose synonymy he placed *P. levior*. In both cases the specimens appear to have been male.

A series of similar cases is easily found in the already confused scheme of *Pomacea* forms. To what extent are many of the mentioned differences among nominal species due to an unnoticed sex dimorphism? Knowledge of many South American species of *Pomacea* is based on nothing more than a few empty shells, without any assessment of variability. A test for the presence of a dimorphic condition in the other apple snails would improve the understanding of the conchological species: several putative species could prove to be sex-based synonyms.

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[3] It should be noted that the sex ratio balance was tipped in favor of the females in the populations of *Marisa cornuarietis* studied by DEMIAN & IBRAHIM (1972).

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The Use of Tetracycline Staining Techniques to Determine Statolith Growth Ring Periodicity in the Tropical Loliginid Squids *Loliolus noctiluca* and *Loligo chinensis*

by

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Abstract. The tropical near-shore loliginid squids *Loliolus noctiluca* and *Loligo chinensis* have statolith growth rings similar to those described for other squid species. These rings also appear to be similar in appearance to increments found in fish otoliths. Daily periodicity of these rings was validated by staining the statoliths with tetracycline and comparing the number of rings produced with the elapsed days. These results were considered in relation to previous validation work on statolith rings that has been carried out with other squid species. Microstructural examination of statoliths promises to be a useful tool to obtain future growth information for these tropical loliginid squids.

INTRODUCTION

Growth rings within the statolith microstructure of the pelagic squids are gaining increased attention as possible chronological time marks. Currently there is a considerable lack of knowledge on the population dynamics of many squid species; basic biological information is lacking on life span, age at maturity, and growth rates. Research on statolith growth increments promises to yield a useful tool to obtain some of this vital information. However, unequivocal demonstration of periodicity in these growth rings is essential.

Statolith growth rings have been observed and counted in several squid species (HURLEY & BECK, 1979; KRISTENSEN, 1980; ROSENBERG *et al.*, 1981; NATSUKARI *et al.*, 1988) and daily ring periodicity has been documented in some (HURLEY *et al.*, 1985; LIPINSKI, 1986; JACKSON, 1989, 1990). The purpose of this study was to investigate statolith ring periodicity in two other tropical loliginids, *Loligo chinensis* (Gray, 1849) and *Loliolus noctiluca* (Lu *et al.*, 1985), using tetracycline staining techniques. *Loligo chinensis* is found throughout much of the tropical Indo-Pacific (ROPER *et al.*, 1984) while *Loliolus noctiluca* is a smaller near-shore

species that is found along the east coast of Australia from New Guinea to Tasmania (LU *et al.*, 1985).

MATERIALS AND METHODS

Loliolus noctiluca

Young individuals of *Loliolus noctiluca* were captured using 1-mm and 8-mm mesh seine nets off the beach at Townsville, North Queensland, Australia. Captured squids were transported back to the laboratory in 20-L plastic buckets and their statoliths were stained by exposing them to an ambient solution of 250 mg of tetracycline per liter of seawater as described in JACKSON (1989). Squids were captured in June and July 1989 and were maintained alive until sacrificed after 30 and 31 days, respectively, although some mortality occurred during maintenance. Squids were kept outside in a 1500-L round fiberglass tank connected to a recirculating seawater system. Three squids captured in June were transferred to a 308-L round tank on day 30 and allowed to grow until they died after 77 and 83 days. Food was supplied *ad libitum* by maintaining live sergestid shrimps *Acetes sibogae australis* (<3
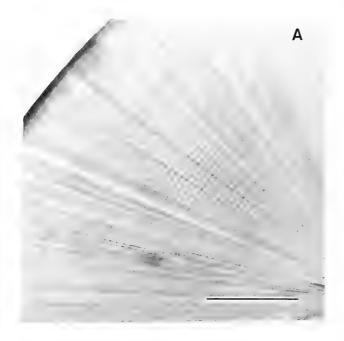
Figure 1

A. Daily growth rings in a whole statolith of a field-captured *Loliolus noctiluca* (female, 59 days, 52 mm dorsal mantle length) mounted in thermoplastic cement. Scale bar = 50 μm. B. Daily growth rings in a whole statolith of a field-captured *Loligo chinensis,* which has been ground and polished on both sides to produce a thin section (male, 78 days, 110 mm dorsal mantle length). Scale bar = 100 μm.

cm in length) with the squids. Large schools of this easily obtainable food source were maintained with *Loliolus noctiluca* and used as a constant and abundant food supply.

Loligo chinensis

Individuals of *Loligo chinensis* were trawled using 40-mm mesh, paired otter trawls in Cleveland Bay off Townsville on 13 July 1989. Although individuals were often killed during trawling, any squids that were in good condition were placed immediately in a 98-L tub with flow-through seawater. Although mortality was high, there was some survival during the course of the day. Because *Loligo chinensis* is large and sensitive to handling, exposing it to an ambient solution of tetracycline-seawater was not suitable; therefore, an injection technique was used. Squids brought back from trawling were injected with a tetracycline-seawater solution (6 mg/mL) at the base of arm I. Previous injection trials indicated that tetracycline was incorporated into the statolith within at least 15 hr of injection, *e.g.,* an individual that was injected in the evening of the day of trawling and found dead the following morning had already taken up the tetracycline into its statolith.

Two individuals of *Loligo chinensis* survived capture and injection and were maintained for 21 and 25 days, respectively, in a 2500-L circular tank that was maintained outside and equipped with a closed recirculating seawater system. Live food organisms kept with the squids were fishes of the families Ambassidae, Mugilidae, and Sillaginidae and juvenile penaeid and *Acetes* crustaceans. Feeding was *ad libitum.*

Statolith Observation

Details regarding grinding techniques, delineation of the tetracycline mark, and counting of subsequent growth rings are the same as described for *Sepioteuthis lessoniana* (JACKSON, 1990). Growth rings in the statoliths of *Loliolus noctiluca* were counted directly without any grinding or polishing, as growth ring definition is excellent in statoliths that are not ground (Figure 1a). Rings were most visible in the dorsal dome region. Similarly the outermost rings could be visualized on the dorsal dome of the statolith of the larger *Loligo chinensis* without any polishing or grinding. However, the statolith of the second individual required grinding and polishing on both sides to enhance the visibility of the growth rings. This resulted in the growth rings being most easily delineated on the rostrum. To delineate all the growth rings clearly within the statolith microstructure of *Loligo chinensis* generally requires grinding and polishing of the statolith on both surfaces to produce a thin section (Figure 1b).

RESULTS AND DISCUSSION

The mean value obtained from replicate growth ring counts from the tetracycline mark to the statolith edge for both *Loliolus noctiluca* (Table 1) and *Loligo chinensis* (Table 2)

Table 1

Tetracycline staining and statolith ring counts for *Loliolus noctiluca* (SD = standard deviation).

Sex	Mantle length (mm)	Date stained	Date experiment terminated	Number of days	Replicate statolith ring counts	Mean	SD
F	35.0	6 June 1989	20 June 1989	14	14, 14, 13	14	0.58
J	19.8	6 June 1989	21 June 1989	15	15, 14, 16	15	1.00
F	38.0	7 June 1989	7 July 1989	30	30, 29, 28	29	1.00
M	32.0	7 June 1989	7 July 1989	30	28, 27, 28	28	0.58
F	34.0	7 June 1989	7 July 1989	30	29, 29, 31	30	1.15
M	30.0	7 July 1989	7 August 1989	31	30, 30, 31	30	0.58
M	38.0	7 June 1989	23 August 1989	77	79, 75, 75	76	2.31
F	45.0	7 June 1989	30 August 1989	83	86, 82, 89	86	3.51
F	54.0	7 June 1989	30 August 1989	83	77, 82, 84	81	3.61

corresponded to, or was very close to, the number of days the squids were maintained. Individuals of *Loliolus noctiluca* were maintained for periods of 13 to 83 days. The degree of correspondence between the days maintained and ring number decreased and the among-count variance increased with the length of time maintained. This reflects the problems associated with counting large numbers of relatively narrow rings.

Statolith growth ring analysis promises to be the most useful method for establishing squid age. However, the technique is of value only when ring counts are highly accurate, which requires experience and familiarity with the ring structure of the species studied.For example, validation of daily rings in *Sepioteuthis lessoniana* has highlighted the presence of sub-daily rings (JACKSON, 1990), which if counted would lead to an over estimation of squid age. Because of the specificity involved in ring counting, it is often difficult to obtain independent counts from multiple observers. Avoiding observer bias is therefore important. This is most easily achieved by using a hand counter during counts so the observer is not biased by previous trials. In addition, replicate counts should be made of each statolith to provide estimates of variance in ring numbers. It would be of use in future work to establish a core of cephalopod workers with expertise and experience in statolith ring counting. In this way both the intra- and inter-observer counting biases could be addressed systematically.

The growth rings present in the squid statolith are similar to those found in fish otoliths. Having the ability to obtain accurate age estimates from fishes has proven to be valuable to the understanding of their biology (*e.g.,* CAMPANA & NEILSON, 1985). It is becoming increasingly apparent that squid statoliths can be used in a similar way to ascertain important biological parameters that would be difficult to obtain by other means (*e.g.,* NATSUKARI *et al.,* 1988). However, the results obtained are only tentative until the periodicity of statolith growth rings can be calibrated.

Techniques used in the analysis of growth ring data from fish otoliths can be applied to the study of statolith microanatomy. These include delineation of growth rings using scanning electron microscopy on polished and etched statolith surfaces (RADTKE, 1983; HURLEY & BECK, 1979; LIPINSKI, 1986). Alternatively, light microscopy has been used to observe growth rings in whole untreated statoliths (BALCH *et al.,* 1988; JACKSON, 1989) or in statoliths that have been ground and polished using various techniques (KRISTENSEN, 1980; ROSENBERG *et al.,* 1981; NATSUKARI *et al.,* 1988; JACKSON, 1990).

Artificially inducing a chemical time mark on the statolith is perhaps one of the most convenient methods for the validation of daily statolith ring periodicity. Culturing squids from hatching (thereby knowing the age of individuals) is the only other means to calibrate ring periodicity (*e.g.,* YANG *et al.,* 1986), and this method is often quite difficult and time consuming. Exposing squids to an ambient solution of tetracycline or calcein-seawater is most easily used with small individuals that can easily be maintained in relatively small confines during the staining process, with minimal damage, *e.g., Idiosipius pygmaeus*

Table 2

Tetracycline injection and statolith ring counts for *Loligo chinensis* (SD = Standard Deviation).

Sex	Date injected	Date experiment terminated	Number of days	Replicate statolith ring counts	Mean	SD	Area of statolith observed
M	13 July 1989	7 August 1989	25	24, 26, 26, 26, 23, 24	25	1.33	Rostrum
M	13 July 1989	3 August 1989	21	20, 20, 20, 22, 21, 22	21	0.98	Dorsal dome

Table 3

Summary of species and number of individuals used in chemical staining of statoliths for the determination of ring periodicity.

Species	Number of individuals	Chemical used	Technique employed	Reference
Illex illecebrosus	4	strontium	given with food	HURLEY *et al.*, 1985
Illex illecebrosus	8	strontium-tetracycline	with food, force feeding	DAWE *et al.*, 1985
Alloteuthus subulata	11	tetracycline	injection	LIPINSKI, 1986
Idiosepius pygmaeus	6	tetracycline	ambient exposure	JACKSON, 1989
Sepioteuthis lessoniana	7	tetracycline-calcein	ambient exposure	JACKSON, 1990
Loliolus noctiluca	9	tetracycline	ambient exposure	Jackson, this report
Loligo chinensis	2	tetracycline	injection	Jackson, this report

(JACKSON, 1989) and juvenile *Sepioteuthis lessoniana* (JACKSON, 1990). However, larger more active species are too sensitive for this type of method, and such other techniques as injection (LIPINSKI, 1986) or inclusion of a statolith-staining drug in the food have been used (DAWE *et al.*, 1985; HURLEY et al., 1985).

Evidence for daily periodicity in statolith growth rings, derived from chemical marking experiments, now exists from 47 individuals out of five species of squids and one sepioid (Table 3). There is considerable scope to extend ring validation work to other cephalopod species, as the species that have been worked on represent only a minute portion of the total cephalopod fauna. Ring validation work on the larger oceanic squids is particularly needed as statolith growth ring analysis promises to be one technique that can be used to establish important biological parameters for many of these species. Furthermore, it is necessary to increase the sample size of validated individuals to extend age validation work beyond the scope of preliminary findings.

It can only be assumed that the statolith ring deposition process that has been observed for *Loliolus noctiluca* and *Loligo chinensis* under these artificial conditions is similar to what occurs in the natural environment. The maintenance conditions were especially suitable for providing a good environment for statolith incremental growth, since the tanks were located outside and thereby exposed to the natural diel light regime. Furthermore, the tanks were relatively large, which promoted a more natural behavior of the squids, especially *Loliolus noctiluca* that appeared to live and grow relatively undisturbed in the tanks. The demonstration of daily statolith rings in *Loliolus noctiluca* and *Loligo chinensis* indicates that these structures will be useful in determining important age and growth parameters for these tropical squids.

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The Eastern Pacific Species of the Bivalve Family Spheniopsidae

by

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Abstract. The Spheniopsidae contains only a few fossil and at least four uncommon living species. The type species of *Spheniopsis, S. scalaris,* from the middle Oligocene of Germany, is discussed and figured. *Spheniopsis frankbernardi,* a new species, is described from the Panamic province and compared to *S. mississippiensis* from the lower Oligocene, *S. americana* from the early Miocene, and *S. triquetra* from the Recent fauna, all of the eastern United States. *Grippina californica* occurs from California to Costa Rica; *G. berryana* is a synonym. *Grippina aupouria* (Powell, 1937) occurs in New Zealand. Recent spheniopsids probably all brood their young.

INTRODUCTION

Among the materials on the work table of the late Frank R. Bernard were some notes about the Recent eastern Pacific species of the Spheniopsidae. He noted that some lots represented a new species, which is here named for him. As evidenced in a draft manuscript, Bernard intended to erect a new family based on *Grippina.* I have examined this question and decided against doing so.

In a handbook on geology by WALCHNER (1846–1851), a listing of the fossils from the middle Oligocene of the Mainz Basin in Germany was provided by BRAUN (1851). Here Braun (p. 1114) made available, with a minimal description[1] and no figure, a new, minute species of *Corbula, C. scalaris.* Its type locality is "Weinsheim" (Weinheim, near Alzey, Rheinland-Pflaz), Germany (49°45′N, 8°6′E).[2]

In his treatment of the Mainz Basin fauna, SANDBERGER (1861:pl. 22, fig. 1–1b; 1863:286) established a new genus, *Spheniopsis,* for *Corbula scalaris,* which he illustrated with three line drawings.[3] NEUFFER (1973:86–87; pl. 9, figs. 3, 4a–b) discussed this species, based in part on Sandberger's

material. Additional species of this genus have been described from the Oligocene of Germany; NEUFFER (1973) lists these, including the similar *S. curvata* KOENEN (1894: 1313–1315; pl. 92, figs. 9a, b, 10a–c, 11a–c) from the lower Oligocene.[4]

Through the kindness of Dr. Ronald Janssen of the Natur-Museum in Senckenberg, I was able to examine and photograph specimens of *Spheniopsis scalaris* from its type locality (SMF 308 404a, b) (Figure 1). The shells of this species, which attain a length of about 4 mm, are elongate, with a pointed, truncate posterior end. Both valves have about 11 conspicuous, rounded concentric ribs, with wide interspaces. The ribs are lower dorsally and posteriorly. The posterior end has two radial ribs, one just below the posterodorsal margin and a second just ventral to this; the area between them is smooth and produced posteriorly to form the truncate end. The dorsal posterior ridge sets off a conspicuous, smooth escutcheon; the lunule is smooth, but less demarcated. The right valve has a short, peglike anterior tooth on the medial end of a thin, subdorsal ridge, and an elongate posterior tooth[5]; the anterodorsal margin of the left valve fits into a groove just above the short anterior tooth. On the hinge plate between the teeth is a shallow, posteriorly directed resilifer. There is no nymph

---

[1] "*Corbula scalaris* A. Braun. Very small (1.5‴ long) [3.3 mm], rostrate, step-like ribbed species, related to *Corbula cuspidata* Brongn. Phil.: sand near Weinsheim; very rare."
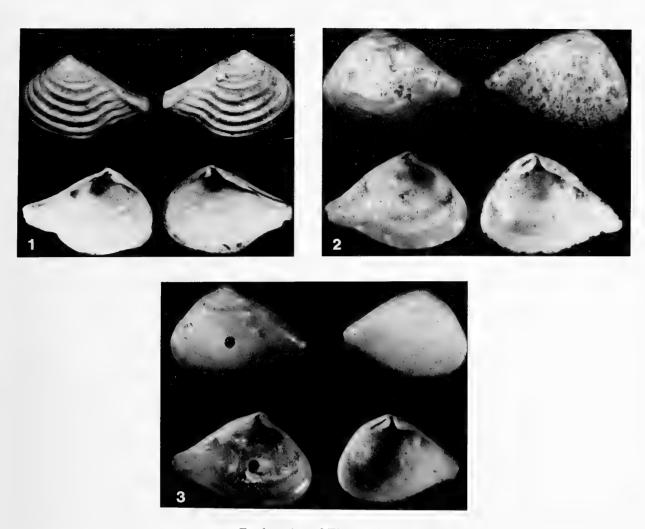
[2] Not to be confused with Weinheim, Baden-Würtemberg. This species was incorrectly listed by KEEN (1969:699) as being from Austria.

[3] The genus is first made available on the explanation to plate 22, which appeared in 1861.

[4] KEEN (1969:699) lists this genus as occurring as early as the middle Eocene, but I am unable to locate any records in Europe or North America earlier than the early Oligocene (R. Janssen and D. Dockery, in letters, 8 December and 29 November 1989, respectively).

[5] I do not know whether these teeth should be called cardinals or laterals, and so I have avoided both terms.

Explanation of Figures 1 to 3

Figure 1. *Spheniopsis scalaris*, SMF 308 404a, right valve; SMF 308 404b, left valve; middle Oligocene; Weinheim, Rheinland-Pfalz, Federal Republic of Germany; length of each, 2.7 mm.

Figures 2, 3. *Spheniopsis americana*. Figure 2: USNM 445737 (right valve) and USNM 445738 (left valve), paralectotypes figured by DALL (1903); length of each, 3 mm. Figure 3: USNM 114679, **lectotype herein**, right valve, length, 2.6 mm; USNM 445736, left valve, paralectotype, length, 2.9 mm.

for the attachment of an external ligament. In the left valve, there is a socket for the anterior tooth; the posterior valve edge rests between the dorsal margin of the right valve and its elongate posterior tooth. There is a short, broad pallial sinus.

MEYER (1887:53–54, 56; pl. 3, figs. 16–16b) described *Mikrola mississippiensis*, a new genus and species, from the lower Oligocene and Bluff Formation of Mississippi. He compared it to *Spheniopsis*, stating that the dentition of the right valve was "entirely different." For many years, *Mikrola* remained a mystery because of Meyer's sketchy figures, and KEEN (1969:637) synonymized it with the semelid genus *Cumingia*. DOCKERY (1982:100–101; pl. 51, figs. 9–15) illustrated two syntypes of *M. mississippiensis* (USNM 645099, 645100) and other material, and syn-

onymized *Mikrola* with *Spheniopsis*. The posterior tooth in the right valve of this species is much shorter than that in *Spheniopsis scalaris*, its posterior end is less produced, and the posterior slope is not set off by radial ridges. Other workers may choose to recognize *Mikrola* as a separate genus or subgenus based on these differences. *Spheniopsis mississippiensis*, which attains only about 3 mm in length, has about 15 conspicuous concentric ribs on each valve.

Spheniopsis mississippiensis, with its relatively short posterior tooth, is close to the only other North American fossil species in this genus, *S. americana* DALL (1903:1508; pl. 57, figs. 28, 29), from the Chipola Formation of Calhoun County, Florida. Dall regarded this formation as being of Oligocene age, but it is now regarded as being of early Miocene age (VOKES, 1989). *Spheniopsis americana*

has fine concentric sculpture. The type material consisted of six syntypes. Dall figured the two largest specimens (USNM 445737 and 445738), both measuring 3 mm; because of their slightly different shapes and differing patterns of wear (Figure 2), they probably do not represent a pair. Because both of these valves are significantly eroded, **I here select as lectotype** a somewhat smaller right valve, measuring 2.6 mm, that is in good condition and shows the characters of the species (USNM 114679), figuring it with a paralectotype left valve in equally good condition (USNM 445736) (Figure 3). The remaining two paralectotypes are USNM 445739 and 445740.

In her discussion of *Spheniopsis americana*, GARDNER (1928:236–237; pl. 36, figs. 9, 10) established a new family for this genus on the grounds that it is distinct from the Corbulidae, species of which have a projecting resilifer in the left valve and a sunken one in the right valve.

Spheniopsids are always minute, and examination of a dried animal of the Recent eastern Pacific *Grippina californica* (LACM 72-120.1) shows that at least this species broods its young; it is not unreasonable to assume that they all do. They may thus represent a line of brooders derived from the Corbulidae, a family that is known from the Upper Jurassic (KEEN, 1969:692). Spheniopsids have remained small, as is the case with many other bivalve brooders, such as members of the Cyamioidea, Galeommatoidea, Condylocardiidae, Bernardinidae, and Turtoniidae, and some Carditidae and Veneridae (see list in SHASTRY, 1979, and family reviews in BOSS, 1982). None of the material presently available of eastern Pacific members of this family is suitable for further anatomical analysis.

The ligament of Recent spheniopsids seems very solid (Figure 12a) and calls to mind the lithodesma of some members of the Thracioidea and the Galeommatoidea, but further study would be required to demonstrate whether it is calcified.

After this paper was accepted for publication, I learned from Dr. Donald R. Moore (verbal communication, 7 June 1990) that three or four living species of *"Spheniopsis"* in the western Atlantic are currently under study. Indeed, a name is available for one of these: *Montacuta triquetra* VERRILL & BUSH (1898:782–783, 894; pl. 91, fig. 3), which has yet to be adequately illustrated, from 79 m off Cape Hatteras, North Carolina.

EASTERN PACIFIC TAXA

Superfamily MYOIDEA

Family SPHENIOPSIDAE Gardner, 1928

Spheniopsis SANDBERGER, 1861:pl. 22, fig. 1–1b [1863: 289]

Type species: *Corbula scalaris* Braun, *in* WALCHNER, 1851:1114; by monotypy.

=*Mikrola* Meyer, 1887 [Type species: *M. mississippiensis* Meyer, 1887; by monotypy].

Shell elongate, posterior end produced, truncate. With anterior and posterior teeth in the right valve; posterior tooth elongate to short; left valve without teeth; laterally elongate ligament present. Sculpture of fine to coarse concentric ribs, sometimes with radial rays defining posterior slope. Pallial sinus short, broad.

Spheniopsis frankbernardi Coan, sp. nov.

(Figures 4–6)

Description: Shell small (to 3.2 mm; holotype), thick, elongate, sharply rounded anteriorly; produced, with rounded truncation posteriorly. Surface with fine concentric sculpture (15–35 ribs; holotype with 30–35 ribs). Right valve with short, thick anterior and posterior teeth on medial ends of subdorsal lamellae, with anterior lamella longer; short, posteriorly oblique resilifer on hinge plate between teeth. Left valve with narrow dorsal margins, without teeth, fitting into subdorsal grooves of right valve. Lunule and narrow, sharply defined escutcheon present. Pallial sinus short, broad.

Type material: LACM 2427, holotype, pair; length 3.2 mm; height. 2.3 mm; convexity, 2.0 mm (Figure 4). LACM 2428, paratype A; length, 2.5 mm (Figure 5). LACM 2429, paratype B; length, 2.6 mm (Figure 6).

Type locality: Off Cabo San Lucas, Baja California Sur (22°8′N, 110°W); 18–37 m, on sand; P. Oringer and L. Marincovich, 4 April 1966; LACM Loc. 66-14.

Distribution: From Punta San Pablo, on the Pacific Coast of Baja California Sur (27°12′55″N, 114°27′30″W) (LACM 71-177.1), to Cabo San Lucas (type locality), into the Gulf of California as far north as Puertecitos, Baja California [Norte] (30°20′N, 119°39′W) (LACM 64-31.1), and south to Playas del Coco, Guanacaste Province, Costa Rica (10°33′N, 85°42′W) (Skoglund Coll.); 13–91 m (mean, 38 m); the only bottom type recorded—on just two lots—is sand. I have examined 11 lots.

Referred material: LACM 71-177.1—Punta San Pablo, Baja California Sur; 21–24 m, on sand; 1 specimen.
LACM 71-178.2—Punta San Pablo, Baja California Sur; 21–30 m; 1.
LACM 2427–2429—Type lot—LACM Loc. 66.14—Cabo San Lucas, Baja California Sur; 18–37 m; 3.
CAS 068038—Isla Partida, near Isla Espíritu Santo, Baja California Sur; 91 m; 1. Cited by KEEN (1971) as *Grippina berryana*.
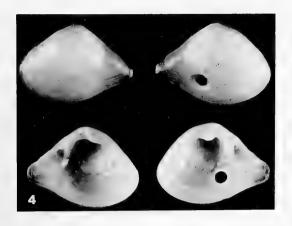LACM 37-191.1—Isla Tortuga, Baja California Sur; 82 m; 3.
SBMNH 35150—Bahía de Los Angeles, Baja California [Norte]; 15–29 m; 5.
SBMNH 35151—Bahía de Los Angeles, Baja California [Norte]; 22–38 m; 3.
LACM 64-31.1—Puertecitos, Baja California [Norte]; 7–18 m; 1.

Explanation of Figures 4 to 6

Figures 4–6. *Spheniopsis frankbernardi* Coan, sp. nov., **herein**. Figure 4: holotype, LACM 2427; length, 3.2 mm.
Figure 5: paratype A, LACM 2428; length, 2.5 mm. Figure 6: paratype B, LACM 2429; length, 2.6 mm.

SBMNH 35152—Teacapan, Sinaloa; 51–60 m; 2.
Skoglund Coll.—Bahía Santiago, Colima; 6–30 m; 5.
Skoglund Coll.—Playas del Coco, Guanacaste Province,
Costa Rica; 30–37 m; 2.

Discussion: This species differs from *Spheniopsis scalaris*
and *S. curvata* in having a thicker shell, less elevated con-
centric ribs, a less produced and less abruptly truncate
posterior end, a posterior slope not defined by radial ribs,
and a shorter posterior tooth in the right valve. It differs
from *S. mississippiensis* in having less elevated concentric
ribs and a less produced posterior end. It differs from *S.
americana* in having a thicker shell, a less produced pos-
terior end, and more conspicuous sculpture. It differs from
S. triquetra, which is thus far known only by the holotype
(USNM 77627), a pair measuring 2 mm in length, in
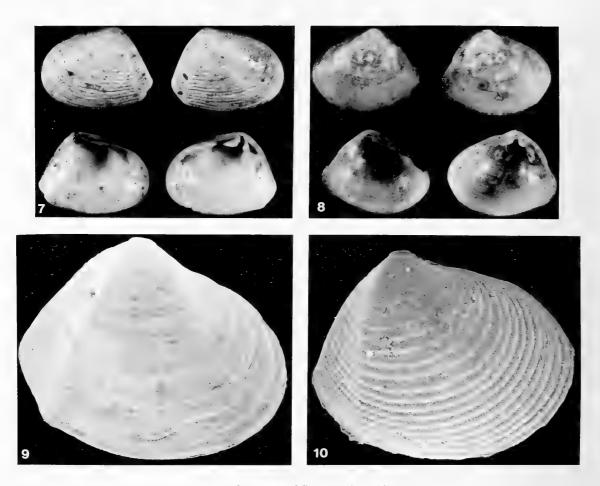being larger, proportionately longer and heavier, in having

thicker, more ventrally directed teeth in the right valve,
and in retaining sculpture on its umbones. More detailed
study of western Atlantic material (D. R. Moore, in prep-
aration) should provide additional points of comparison.

Grippina DALL, 1912:128.
   Type species: *G. californica* DALL, 1912:128; by original
      designation.

   Similar to *Spheniopsis* but with a broadly truncate pos-
terior end that is not produced. Posterior slope defined by
two low radial ridges. With short anterior and posterior
lateral teeth in the right valve; left valve without teeth.
Sculpture of fine to coarse concentric ribs, or smooth. Pal-
lial sinus short, broad.

   This genus is thus far known from the Pleistocene and
Recent faunas in the eastern Pacific and the Recent fauna
of New Zealand.

Explanation of Figures 7 to 10

Figures 7–10. *Grippina californica.* Figure 7: holotype of *G. californica,* USNM 214362; length, 2.6 mm. Figure 8: holotype of *G. berryana,* CAS 064756; length, 2.3 mm. Figure 9: LACM 72-114, northwest end of Isla Cedros, Baja California [Norte]; 14 m; length, 2.0 mm. Figure 10: SBMNH 35153, Cuastecomate, Jalisco, Mexico; 12–30 m; length, 1.8 mm.

Grippina californica Dall, 1912

(Figures 7–12)

Grippina californica DALL, 1912:128; OLDROYD, 1925:205; pl. 15, figs. 1—3; LAMY, 1941:15, unnumbered fig.
Grippina berryana KEEN, 1971:269–270, 943; fig. 693.

Type material and localities: *G. californica*—USNM 214362, holotype, pair; length, 2.6 mm; height, 2.0 mm; thickness, 1.4 mm (Figure 7). Off San Diego, San Diego Co., California (32°40′N, 117°14′W); 29–37 m; C. W. Gripp.
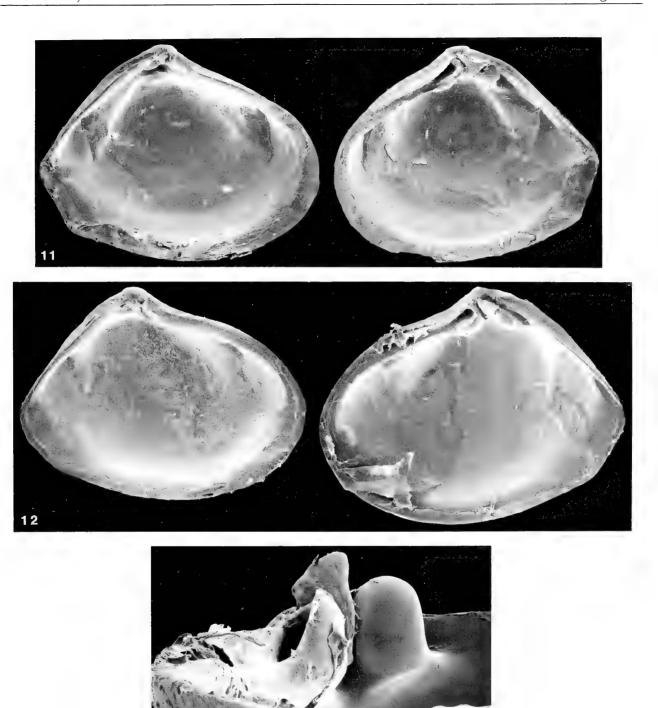
G. berryana—CAS 064756, holotype, pair; length, 2.3 mm; height, 1.9 mm; convexity, 1.4 mm (Figure 8); CAS 064757, paratype, worn left valve; SBMNH 34819, paratype, one worn pair. Northwest side of Bahía Salinas, Isla Carmen, in the Gulf of California, Baja California Sur (25°59′N, 111°8′W), in 5–9 m; J. Fitch.

Description: Small (to 2.8 mm; CAS 068036; Isla Guadelupe, Baja California [Norte]), quadrate to trigonal; posterior end broadly truncate, not greatly produced. Sculpture somewhat variable, with heavy concentric ridges in some specimens, almost smooth in others. With short anterior and posterior teeth in right valve, and with anterior tooth on medial end of long subdorsal lamella; posterior end without such a lamella; narrow, posteriorly oblique resilifer present between teeth; left valve without teeth. Pallial sinus short, broad.

Additional specimens are illustrated with SEM micrographs (Figures 9–12).

Distribution: Southeast of Santa Cruz Island, Santa Barbara Co., California (33°55′47″N, 119°31′5″W) (LACM 48-43.2), to northwest end of Isla Cedros, Baja California [Norte] (28°21′N, 115°15′W) (LACM 72-114); in the Gulf of California as far north as Punta Gorda, Baja California

Explanation of Figures 11 and 12

Figures 11, 12. *Grippina californica.* Figure 11: LACM 71-93, southeast end of Isla Cedros, Baja California [Norte]; 73–91 m; length, 2.3 mm. Figure 12: SBMNH 35153, Cuastecomate, Jalisco, Mexico; 12–30 m; length, 2.0 mm; Figure 12a: close-up of right valve showing ligament between teeth; view is oblique from anterior end.

Sur (23°5′N, 109°35′W) (LACM 66-18.2), south to Isla del Cano, Puntarenas Province, Costa Rica (8°43′15″N, 83°53′7″W) (LACM 72-63.3); from the intertidal zone to 42 m (mean, 16 m), among sand or rubble. I examined 19 Recent lots, including the type specimens. It has been recorded from a late Pleistocene terrace on Santa Barbara Island (LIPPS et al., 1968:297, 299, as "aff. G. californica").

Discussion: Material from the Panamic province, for which the name *Grippina berryana* was proposed, differs from Californian material only in its smaller size (maximum length 2.3 mm) and narrower posterior slope that is less well defined by radial ridges. Additional sampling will probably fill in the distribution from Isla Cedros to the Gulf of California.

A NEW ZEALAND SPECIES

I have recently learned that *Mysella aupouria* POWELL (1937: 172–173; pl. 47, fig. 5) is a *Grippina* (P. A. Maxwell, in correspondence, 1 Dec. 1989). It is more elongate and longer posteriorly than the eastern Pacific species of this genus.

It is possible that additional taxa that have been assigned to *Mysella* will prove to belong to *Grippina*.

ACKNOWLEDGMENTS

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The Molluscan Publications and Taxa of

Lorenzo Gordin Yates (1837–1909)

by

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Abstract. Lorenzo Gordin Yates (1837–1909) was an early amateur naturalist in California, who had a particular interest in malacology. He introduced seven new names for mollusks, of which five are currently regarded as valid. Type material is extant for four of the six species-group taxa.

INTRODUCTION

Lorenzo Gordin Yates was an early Californian naturalist, whose interests covered many fields (Figure 1). His life and contributions were discussed by CAMP (1963a, b) and PILSBRY (1909), and only brief biographical information is given here. The purpose of the present article is to provide a bibliography of his publications in malacology and a listing of the molluscan taxa he made available in them, as well as information about their types and current taxonomic status.

Yates was born on 8 January 1837, in Eastchurch on the Isle of Sheppey, which is in the mouth of the Thames River in England.[1] The son of Richard Owen and Rosetta Mary (Chambers) Yates, he spent his first nine years on that isle, where he began making collections, particularly Eocene fossils, constructing mechanical inventions, and having some education in private schools.

His family moved to America, arriving in New York in 1853.[2] There he engaged in menial jobs until moving in 1854 to Sheboygan, Wisconsin, where he became an apprentice in dentistry to Dr. Edwin M. Thorpe. Here he resumed his natural history collections, commencing correspondence with Spencer F. Baird of the Smithsonian Institution, as did so many amateur naturalists of his day (DALL, 1915).

After plans to study medicine in New York fell through, he traveled and collected extensively in several states, in-cluding Illinois, Indiana, Michigan, Missouri, and Pennsylvania. He settled in Ripon, Wisconsin, where he practiced dentistry. In 1861, he married Eunice Amelia Lake, the daughter of a Ripon College professor. His son Albert Edward was born there in 1862. The next year, the Yates family moved to Fond du Lac, Wisconsin, where his sons Walter Sidney and Frederick William were born in 1863 and 1864, respectively.

In November 1864, the family moved to California by way of Nicaragua, settling in Centerville[3] in Alameda County, now a district of Fremont. He set up a dental practice and engaged in natural history work in his spare time, including some collecting for the California Geological Survey. Sons George Owen and Gordin Ruskin were born in 1866 and 1873, respectively, as well as daughters Florence Rosetta in 1877 and Inez in 1878.

He made an exploratory trip to Santa Rosa Island in spring 1876 (YATES, 1876a).[4] Intrigued by the natural history of the Santa Barbara area and by its social scene, he moved there in November 1881, evidently separating from his wife ("she was all for religion and he all for science").[5] Yates continued both his dentistry and natural history studies in Santa Barbara. Rheumatism curtailed his dental practice by the turn of the century, and he

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[1] His birthday is given as 12 January by CAMP (1963a, b), but the 8th is given in one account seen and presumably approved by Yates himself.

[2] The date of his arrival in the United States is given by CAMP (1963a, b) as 1851, but is given as 1853 in the account seen by Yates.

[3] In Yates' day, this was spelled "Centreville," as it is here in the Literature Cited for the tracts and catalogues published during his residency there. (The date he moved there is given in one source as 1863, but this seems to be in error.)

[4] Yates' diary of the Santa Rosa Island expedition, which was sponsored by the Smithsonian Institution, is archived in the Santa Barbara Historical Society.

[5] From holographic biographical notes by his second wife, now on deposit in the archives of the Santa Barbara Museum of Natural History. His first wife died on 20 February 1898, after a separation of over 17 years.

Figure 1

Lorenzo Gordin Yates, in his Santa Barbara herbarium. Courtesy of the Santa Barbara Historical Society.

endeavored to make a living in natural history by selling specimens and writing articles. He worked on the collections of the Golden Gate Park Museum in San Francisco, forerunner of the DeYoung Museum, for two years in about 1900.[6]

In August 1908, Yates married his widowed dental assistant, Mary Merill Isabella Childs. Five months later, on 31 January 1909, he died in Santa Barbara at the age of 72.

CAMP (1963a, b) discussed Yates' contributions to various fields, including anthropology, archaeology, botany, geology, and vertebrate paleontology. Yates corresponded with scientists throughout the world and was a member of many organizations.
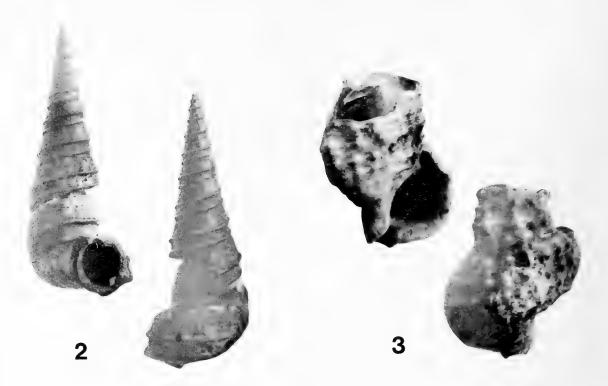
One of Yates' chief interests was malacology, and he amassed large collections of Recent and fossil mollusks. He issued a number of sales catalogs of his material, and he wrote articles on malacological topics, including faunal lists for the Santa Barbara area and descriptions of a few new species.

In the summer of 1872, he sold a substantial part of his mollusk collection to Wabash College in Indiana for $3000. This institution retains an inventory of the shipment, but only a few specimens from Yates remain in the collection. Curators there believed that much of the material had been transferred to Earlham College, also in Indiana, in the 1950s (E. C. Williams, letter, 26 August 1988). However, this was evidently not the case (J. Iverson, letter, 1 October 1988), nor was the material acquired by the Field Museum in Chicago (G. A. Solem, letter, 3 February 1989), as others had thought.

Yates tried to interest various institutions in acquiring his natural history collections. Early in 1893, he loaned part of his shell collection to Stanford University, where it remained for seven years. In September 1893, he taught at the Froebel Institute in Los Angeles, taking some of his collections there. Later, he tried to interest Mills College in Oakland, California, in purchasing his collections for $30,000, but the college refused, as did the cities of Santa Cruz and Los Angeles. In the meanwhile, he sold many of his finest specimens.

In 1912, his widow loaned the collections to the Los Angeles County Museum of Natural History, where they remained for more than 20 years. Following her death in

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[6] The natural history materials of the DeYoung Museum were turned over to the California Academy of Sciences when the museum came to specialize in art.

2 **3**

Explanation of Figures 2 and 3

Figure 2. *Vermicularia fewkesi* (Yates, 1890). Holotype of *Vermetus* (*Vermiculus*) *fewkesi*; height = 16 mm; now lost.

Figure 3. Holotype of *Cerithium* (*Vertagus*) *lordii* Yates, 1890; length about 14 mm; now lost.

1936, the collections ended up in the hands of Frank S. Van den Berg. He placed the material in storage in the basement of the Santa Barbara County Courthouse. The Recent mollusks were given by Van den Berg's estate to the Santa Barbara Museum of Natural History in 1948, and the fossil material was given to Santa Barbara State College, now the University of California at Santa Barbara. Much of the material deposited in the Santa Barbara Museum of Natural History was destroyed by fire in 1962.

LIST OF TAXA

The following list includes the taxa that Yates introduced. Each original combination is followed by the original reference (keyed to the Literature Cited). This is followed by type locality (notes in brackets provide additional data), information about type material, and remarks about current allocation. The Literature Cited provides references for Yates' taxa, but not for their senior synonyms; references for his catalogs and papers with material on mollusks not containing new taxa are also included. The following abbreviations are used below:

ANSP—Academy of Natural Sciences, Philadelphia;
SBMNH—Santa Barbara Museum of Natural History;
UCSB—University of California, Santa Barbara, Department of Geology.

alamedense, Pinna—YATES, 1887:[?] [sic, for *alamedensis*]. See also Yates *in* COOPER, 1888:259; COOPER, 1894: 56; pl. 4, fig. 53.
   Alameda Creek, Alameda Co., Calif.; in a sandstone boulder; [San Pablo Group]; Miocene.
   Type material: UCSB Y474, holotype, pair.
   Remarks: This species has generally been dated from Yates *in* COOPER (1888), but it was made available a year earlier in a newspaper account of a meeting of the Santa Barbara Society of Natural History, which is reprinted here in the Appendix.[7]
      Atrina alamedensis (Yates), according to MOORE (1983:80–81; pl. 23, fig. 3; pl. 27, figs. 1, 3).

fewkesi, Vermetus (*Vermiculus*)—YATES, 1890b:48; pl. 2, figs. 8, 9.
   Near Ellwood, Santa Barbara Co., Calif.; A. E. Yates.
   Type material: Lost. A photograph of the original specimen, from which the original line drawing was prepared, was encountered in this study stapled into a reprint of Yates' paper, and it is reproduced here (Figure 2).

[7] This newspaper article and others listed in the Literature Cited are in Yates's scrapbook in The Bancroft Library. We have been unable to find the relevant issues of the newspapers in microfilm archives.

Remarks: *Vermicularia fewkesi* (Yates), according to McLean (1978:30–31; fig. 15.2).

fordii, Venus—Yates, 1890b:46; pl. 1, figs. 1–5.
 Santa Barbara Channel; evidently several specimens.
 Type material: SBMNH 22900, lectotype (Scott *et al.*, 1990:16; fig. 3).
 Remarks: *Globivenus fordii* (Yates, 1890).

indioensis, Helix (Arionta) carpenteri—Yates, 1890e:63.
 Near Indio, San Bernardino [Riverside] Co., Calif.; S. Bowers. Among granite talus, on S side of the valley (Yates, 1890c:52).
 Type material: ANSP 62145, lectotype (Baker, 1962:11); ANSP 77887, SBMNH 03705, paralectotypes.
 Remarks: *Eremarionta indioensis* (Yates), according to Bequaert & Miller (1973:109). Figured in Pilsbry (1939:246–247; figs. 125c, f) in *Micrarionta (Eremarionta)*.

lordii, Cerithium (Vertagus)—Yates, 1890b:46–47; pl. 2, figs. 6, 7.
 Near Ellwood, Santa Barbara Co., Calif.; in a kelp holdfast; A. E. Yates.
 Type material: Lost. A photograph of the original specimen, from which the original line drawing was based, was encountered in this study stapled into a reprint of Yates' paper, and it is reproduced here (Figure 3).
 Remarks: This species remains a mystery. Nothing like it has ever been collected again, and no similar species are reported in deposits of Pliocene or Pleistocene age in southern California. Grant & Gale (1931:758) suggested that it was similar to what is now called *Rhinoclavis (Ochetoclava) gemmata* (Hinds, 1844); however, Houbrick (1978:20, and letter, 18 October 1988) doubts this. There is some resemblance to *Cerithium (Thericium) nicaraguense* Pilsbry & Lowe, 1932, but that species has a smaller shell with a more oblique anterior canal, and it occurs only as far north as Nicaragua. We suspect that Yates' specimen was brought with ballast from another province.

Mitricaria—Yates, 1885c:53.
 Type species: *M. conica* (Schumacher, 1817); monotypy; =*Imbricaria conica* Schumacher, 1817; =*Mitra conularis* Lamarck, 1811.
 Remarks: Synonym of *Imbricaria* Schumacher, 1817.

venturense, Pinna—Yates, 1887:[?] [sic, for *venturensis*].
 See also Yates, *in* Cooper, 1888:259; Cooper, 1894:56; pl. 5, fig. 54.
 Casitas Pass, Ventura Co., Calif.; "Pliocene" [Vaqueros Fm.; Oligocene or Miocene]; several specimens.
 Type material: UCSB Y3096, lectotype (Moore, 1983:80, as "holotype"). Remarks: As with *Pinna alamedensis,* this species was first made available in a newspaper account of a meeting of the Santa Barbara Society of Natural History.[7]

Atrina venturensis (Yates), according to Moore (1983:80; pl. 23, fig. 2; pl. 27, fig. 2).

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[Note: The following three catalogues, first issued in 1885, were reissued in 1886 with different covers, and also bound together. The contents appear to be the same in each reissue. CAMP (1963b) discusses the various versions.]

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APPENDIX

The following is reprinted as it appeared in the *Santa Barbara Independent* sometime in late May or early June 1887. We have been unable to find a microfilm set of this newspaper containing these months to obtain the exact date and page number. This transcript is taken from a clipping in Yates' scrapbook in The Bancroft Library at the University of California, Berkeley. The account is given just as it appeared, except that the generic and specific names have been converted to italics. It differs in only minor ways from the account one year later (Yates *in* Cooper, 1888:259) although the last three paragraphs were not included in the latter.

CALIFORNIA FOSSILS

New Fossil Pinnae of the
Tertiary of California

by Dr. Lorenzo G. Yates

[Paper read before the Santa Barbara
Society of Natural History.]

PINNA, Linn.
Pinna Alamedense, n. sp.

This species has nine concentric inequidistant rounded wrinkles emanating from the open side, and turning toward the hinge at nearly right angles, the entire shell marked by small longitudinal narrow ribs, (about 40) which, radiating from the apex, extend to the basal margin, becoming more indistinct as they approach the lower margin. These ribs at their intersections with the lines of growth are ornamented by slight elevations forming zigzag markings along the lines of growth.

The hinge side is straight the entire length, the opposite side running parallel for about one-half the distance from base to apex, where it makes a sharp curve, thence at an angle of about 45 degrees to the apex. Length nine, width five, and thickness about two inches. Miocene.

Locality, Alameda Creek, Alameda County, California. Only one specimen found, and that a very fine one, in the centre of a round sandstone boulder.

Pinna venturense, n. sp.

From the hinge side to about two-thirds of the width of this shell is marked by nine well developed, narrow ribs, radiating from the apex to the basal margin, the other portion shows rounded, concentric inequidistant ribs extending only to the line of the radiating ribs, so that about two-thirds of the surface is covered by the radiating smaller ribs, and one-third by the curved, concentric, rounded ribs or wrinkles, very like *Pinna pectinata,* of Mont., figured in "Brown's Recent Conchology." *Pinna Venturense* is short and thick compared with its length. The largest specimen found was about five and one-half inches long, three and one-half in width, and one and three-fourths in thickness, the hinge side considerably shorter than the other.

Locality, several specimens collected by the writer in Casitas Pass, Ventura county, California. Pliocene.

One species of fossil pinna from the cretaceous of California was described by W. M. Gabb in the Palaeontology of the California State Geological Survey. This genus was called *Pinna* (a fin or wing) from the resemblance of its byssus, (the filaments by which it attaches itself to other substances) to the plume or aigrette which the Roman soldiers attached to their helmets; while some French call them Jambonneau, from their resemblance, in form and color, to a dried ham. More than one hundred species, recent and fossil, are known. Some of the living species attain a length of two feet, and some fossil species are said to have been three feet in width. They range from low water to a depth of sixty fathoms. In most of the species the shell is thin and translucent, formed almost entirely of prismatic cell-layers.

Pinna nobilis inhabits the shores of the Mediterranean Sea, and is the species from the byssus of which the Maltese and Neapolitans manufacture gloves and other articles; this manufacture was carried out by the ancient Greeks and Romans. Pearls are sometimes found in this species. The Pinnae moor themselves fast and are almost covered by sand, the sharp knife-like edges projecting above the surface, like unto the Anodontas and other fresh water bivalves.

These shells are not found living on the Pacific Coast of the United States, but several species are found on the west coast of Mexico, at least three species at Cape St. Lucas, the southern extremity of the peninsula of Lower California.

Santa Barbara, May 28, 1887.

On *Cochlicopa lubrica* (Müller, 1774) and *Cochlicopa lubricella* (Porro, 1837) (Gastropoda: Pulmonata: Cochlicopidae) in the Sierra de O Courel (Lugo, NW Spain)

by

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Abstract.   Variability of the characters differentiating *Cochlicopa lubrica* from *C. lubricella* belonging to different populations in the Sierra de O Courel (Lugo, Spain) is studied. Noted are overlap in the diameter and height of both species and also a high variability in all the structures of the genital system, confirming the existence of intermediate forms. However, these forms are not in agreement with the description of *C. repentina* Hudec, 1960.

INTRODUCTION

Four species belonging to the genus *Cochlicopa* have been described in Europe: *C. lubrica* (Müller, 1774), *C. lubricella* (Porro, 1837) (synonymy: *C. lubrica* var. *minima* Siemaschko, 1847), *C. repentina* Hudec, 1960, and the rare *C. nitens* (Gallenstein, 1848), which is found only in isolated colonies in central and eastern Europe (KERNEY & CAMERON, 1979). *Cochlicopa lubricella* was long considered to be a variety of *C. lubrica* (GERMAIN, 1930; MERMOD, 1930; ADAM, 1947) until QUICK (1954) redescribed it as a species in its own right. HUDEC (1960) later established further differences between the two species, and introduced *C. repentina* Hudec, 1960, as a new species with characteristics intermediate between those of *C. lubrica* and *C. lubricella.* Most authors currently consider *C. lubrica* and *C. lubricella* to be distinct species, although others find difficulty in distinguishing between the two taxa. The status of *C. repentina* as a separate species is not yet well established (WALDÉN, 1976; GITTENBERGER, 1983).

The collection of specimens of *Cochlicopa* in the Sierra de O Courel (Lugo, Spain) presented many problems of identification. These problems led us to study the variability of the differential characters of *Cochlicopa* populations in this sierra with a view to determining whether all the specimens collected could be definitely identified, on the basis of these characters, as belonging to one or the other of the species mentioned above.

SITES STUDIED

The Sierra de O Courel is located in the northwest of the Iberian Peninsula, in the eastern part of the Province of Lugo (UTM: 29TPH 41/42, 51/52). Six sites in this area were sampled, each site having a different vegetation type: *Quercus pyrenaica* wood; broom scrub (*Genista florida polygaliphylla* and *Cytisus scoparius*); meadow over slate (class *Molinio-Arrhenatheretea,* order *Arrhenatheretalia,* alliance *Cynosurion cristati*); meadow over limestone (class *Molinio-Arrhenatheretea,* order *Arrhenatheretalia,* alliance *Arrhenatherion*); holm-oak wood (*Quercus ilex rotundifolia*); and river bank in potential *Alnus glutinosa* territory. The first three sites lie over slates and the last three over limestone. All are located at an altitude of between 500 and 600 m except the broom scrub, which lies at 1200 m.

MATERIALS AND METHODS

The specimens were collected from samples of litter, in each locality, every three months during two years from December 1982 to October 1984. Immediately after collection, the litter was dried and sieved in the laboratory, and all of the obtained fractions were examined. These specimens were studied from a conchological point of view.

In order to obtain specimens suitable for dissection, some live individuals were collected in the field, immediately drowned and preserved in 70% alcohol (three occasions: 24 September 1983, 19 December 1983, 6 March 1984).

Table 1

Frequency distribution of maximum shell diameters in each population studied (class size, 0.1 mm). HO; holm-oak wood; RB: river bank; SM: slate meadow; LM: limestone meadow; BS: broom scrub; QP: *Quercus pyrenaica* wood.

Shell diameter class (mm)			Frequency in population					
Range	Center	Total	HO	RB	SM	LM	BS	QP
1.75–1.84	1.8	5	5	—	—	—	—	—
1.85–1.94	1.9	47	43	—	3	—	—	1
1.95–2.04	2.0	116	102	4	8	—	—	2
2.05–2.14	2.1	135	101	25	6	—	2	1
2.15–2.24	2.2	65	45	12	5	—	3	—
2.25–2.34	2.3	32	8	14	6	1	3	—
2.35–2.44	2.4	23	—	19	7	3	4	—
2.45–2.54	2.5	25	—	13	9	3	—	—
2.55–2.64	2.6	28	—	15	6	7	—	—
2.65–2.74	2.7	17	—	11	1	5	—	—
2.75–2.84	2.8	13	—	6	1	6	—	—
2.85–2.94	2.9	1	—	1	—	—	—	—
2.95–3.04	3.0	3	—	—	—	3	—	—
3.05–3.14	3.1	1	—	—	—	1	—	—
Shells measured		511	304	110	52	29	12	4
Mean (mm)		2.19	2.05	2.38	2.30	2.68	2.28	2
SD		0.25	0.10	0.24	0.24	0.20	0.11	0.08
χ^2		235.6	1.70	41.2	11.6	6.8	2.9	—

The height and maximum diameter of the shells of 511 adults were measured and their morphological characteristics recorded (adults were identified by the thickening of the peristome). The corresponding frequency distributions were established for each population and subjected to a χ^2 test of normality. The correlations between height and diameter were calculated, and the different correlations were compared in terms of the standard error of the differences using Fisher's *z* function (SOKAL & ROHLF, 1980).

The genitals of 43 specimens from various populations were drawn with the aid of a camera lucida.

Once examined, all specimens were deposited in the collection of the Department of Animal Biology (Zoology) of the University of Santiago (DZUS).

RESULTS

Shells

The total distributions of both the heights and diameters of the shells were far from normal. The distribution of diameters was bimodal (Table 1) and the distribution of heights was strongly skewed to the right (Table 2).

In the holm-oak wood population, both distributions were unimodal and symmetrical (Figure 2), and their ranges (1.75–2.34 mm for diameters and 4.1–5.89 mm for heights) match those published for *Cochlicopa lubricella*. The morphology of these shells also fits the description of *C. lubricella*: the whorls are less tumid with shallow sutures, axial growth lines are obvious, and the peristome has a light-colored inner edge (Figure 1). The *Quercus pyrenaica* wood population can similarly be identified as *C. lubricella*.

The limestone meadow shells agree fairly well with the description of *Cochlicopa lubrica*: the whorls are tumid, with fairly deep sutures and thin axial growth lines, and
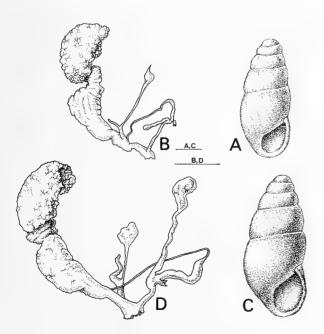

Figure 1

Typical shells and genitalia from the holm-oak wood *Cochlicopa lubricella* populations (A, B) and the limestone meadow *C. lubrica* population (C, D). Scales, 1 mm.

Table 2

Frequency distribution of shell heights in each population studied (class size, 0.2 mm). Abbreviations as in Table 1.

| Shell height class (mm)			Frequency in population					
Range	Center	Total	HO	RB	SM	LM	BS	QP
4.10–4.29	4.2	2	1	—	—	—	1	—
4.30–4.49	4.4	28	22	2	2	—	1	1
4.50–4.69	4.6	55	43	4	6	—	1	1
4.70–4.89	4.8	89	69	5	7	—	7	1
4.90–5.09	5.0	94	75	7	9	1	1	1
5.10–5.29	5.2	88	55	21	8	3	1	—
5.30–5.49	5.4	64	29	24	7	4	—	—
5.50–5.69	5.6	26	7	10	4	5	—	—
5.70–5.89	5.8	17	3	6	6	2	—	—
5.90–6.09	6.0	15	—	9	2	4	—	—
6.10–6.29	6.2	13	—	9	1	3	—	—
6.30–6.49	6.4	11	—	8	—	3	—	—
6.50–6.69	6.6	5	—	3	—	2	—	—
6.70–6.89	6.8	3	—	2	—	1	—	—
6.90–7.09	7.0	1	—	—	—	1	—	—
Shells measured		511	304	110	52	29	12	4
Mean (mm)		5.15	4.95	5.54	5.19	5.88	4.75	4.70
SD		0.50	0.31	0.55	0.45	0.53	0.26	0.26
χ^2		117.4	7.08	23.9	5.4	4.70	6.73	0.92
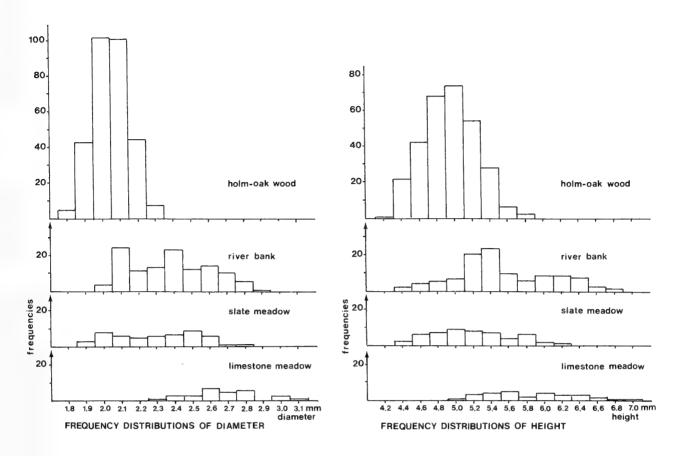
the inner edge of the peristome is reddish brown (Figure 1). The size of these shells was in some cases smaller than is mentioned by other authors, but the ranges (2.25–3.14 mm in diameter and 4.90–7.09 mm in height) were always within that found by QUICK (1954) in the type locality of *C. lubrica* in Frederiksdal (Germany). The irregularity of the profiles of the frequency distributions (Figure 2) may be attributed to the breadth of the ranges and the small number of shells measured; even so, the distributions are close to normal ($P < 0.05$ for height; see Table 2) and the limestone meadow population may be identified as *C. lubrica*.

The limestone meadow is located close to the holm-oak wood, but affords a wetter habitat owing to frequent irrigation. This difference is in keeping with the literature, in which *Cochlicopa lubrica* is considered as typical of wet areas and *C. lubricella* as preferring drier spots (QUICK, 1954; KERNEY & CAMERON, 1979). The diameter ranges of the holm-oak wood and limestone meadow populations overlap only at one extreme (2.3 mm; see Table 1), while the overlap in heights is more extensive (5.0–5.8 mm; see Table 2).

The dimension ranges of the river bank and slate meadow populations cover those of both species. Both types of morphology were found among the shells collected at these sites, as well as shells with intermediate characteristics, and at both sites the frequency distributions are non-normal (Tables 1, 2). These may be deemed accordingly to be mixed populations. In the case of river bank, the pres-

ence of a mixed population might be explained as a result of receiving new individuals in minor floods. However, this reason is not valid for the slate meadow.

In the broom scrub, the range of measured diameters straddled the borderline between the two species, while the measured heights all fell in the smallest six classes. The shells here are stumpy, but otherwise morphologically similar to *Cochlicopa lubrica*. It should be remembered that this population is located at an altitude of 1200 m, where climatic conditions differ from the rest of the localities. Perhaps, this has an influence on the conchological characteristics of these specimens.
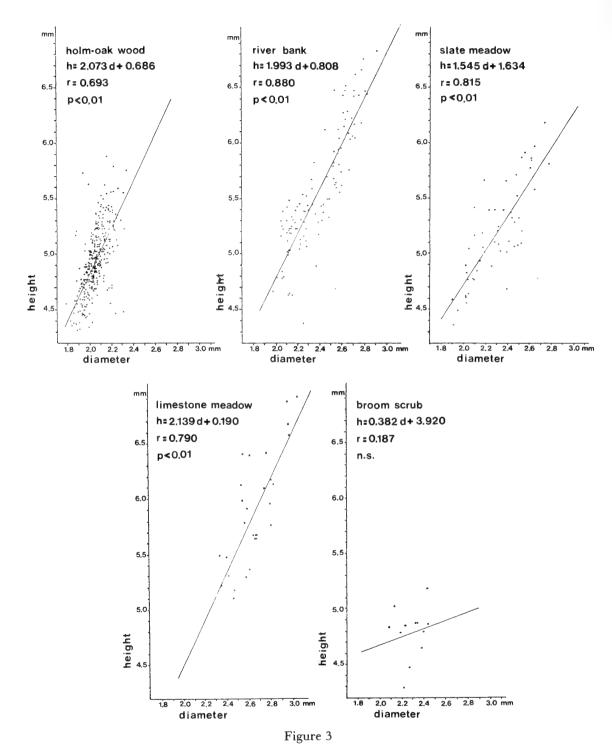
In keeping with the observations of QUICK (1954), the mean of the height-diameter ratio of the holm-oak wood *Cochlicopa lubricella* population is greater than that of the limestone meadow *C. lubrica* population (Table 3). However, the corresponding ranges overlap (the limestone meadow range is in fact contained within the holm-oak wood range), so this ratio is not reliable for identification purposes. Figure 3 shows the correlation between height and diameter for each population; the best correlation was achieved in the mixed populations of river bank and slate meadow. Table 4 lists the standard errors in the differences between significant correlations. The only significant differences are between the holm-oak wood *C. lubricella* population and the river bank mixed population; in particular, there was no significant difference between the holm-oak wood *C. lubricella* population and the limestone meadow *C. lubrica* population.

Figure 2

Frequency distributions of shell diameter and height in the various populations sampled.

Table 3

Frequency distribution of shell height-diameter ratio in each population studied (class size, 0.1).
Abbreviations as in Table 1.

Shell height-diameter ratio class			Frequency in population					
Range	Center	Total	HO	RB	SM	LM	BS	QP
1.85–1.94	1.9	3	1	1	—	—	1	—
1.95–2.04	2.0	10	1	—	3	2	4	—
2.05–2.14	2.1	26	3	4	7	9	3	—
2.15–2.24	2.2	56	11	23	12	8	2	—
2.25–2.34	2.3	122	63	30	19	7	1	2
2.35–2.44	2.4	167	122	33	7	2	1	2
2.45–2.54	2.5	99	80	16	2	1	—	—
2.55–2.64	2.6	26	21	3	2	—	—	—
2.65–2.74	2.7	1	1	—	—	—	—	—
2.75–2.85	2.8	1	1	—	—	—	—	—
Shells measured		511	304	110	52	29	12	4
Mean (mm)		2.36	2.41	2.33	2.26	2.20	2.11	2.35
SD		0.13	0.11	0.12	0.14	0.12	0.14	0.06
χ^2		39.0	47.1	16.0	5.59	2.34	2.49	0.21

holm-oak wood
h= 2.073 d + 0.686
r= 0.693
p<0.01

river bank
h= 1.993 d + 0.808
r= 0.880
p<0.01

slate meadow
h= 1.545 d + 1.634
r= 0.815
p<0.01

limestone meadow
h= 2.139 d + 0.190
r= 0.790
p<0.01

broom scrub
h= 0.382 d + 3.920
r= 0.187
n.s.

Figure 3

Regression of shell height on shell diameter in the populations studied.

Genitals

Figure 4 shows the male genitalia of the examined specimens arranged in three groups by maximum shell diameter: Group 1 (Nos. 1–19), with 1.75–2.24 mm shells in the *Cochlicopa lubricella* range; Group 2 (Nos. 20–40), with 2.35–3.14 mm shells in the *C. lubrica* range; and Group 3 (Nos. 41–43), with 2.25–2.34 mm shells, which is the range of overlap between the two species in the O Courel populations. In every group, ordination was made

Table 4

Values of Fisher's *z* function of correlation coefficient *r* (Figure 3) in each population studied, together with the standard errors of the differences obtained. *, significant at the 95% level. Abbreviations as in Table 1.

Population	*z*	LM	RB	SM
HO	0.849	0.755	4.389*	1.614
LM	1.003	—	1.554	0.388
RB	1.343		—	1.423
SM	1.097			—

according to the locality of collection. In Table 5 the date of recollection and measurements of characters with taxonomic value are indicated.

According to QUICK (1954) and HUDEC (1960), *Cochlicopa lubricella* has relatively small male genitalia. The penis is long and thin, with a thicker distal portion; the epiphallus is no shorter than the penis and merges gradually into the vas deferens; and the penis appendix is roughly as long as the epiphallus, with a thicker distal portion that nevertheless does not amount to a well-differentiated bulb. Except for the small size of the male genitalia and the lack of a well-differentiated bulb, these characters are far from constant in Group 1. In this group, specimens from different localities and dates are included (Table 5). Therefore, these factors are not most important in explaining the variability of the observed characters since this variability is also observed between specimens from the same locality and date.

According to the descriptions of *Cochlicopa lubrica*, its male genitalia are fairly large. The penis is thick; the epiphallus, no shorter than the penis, narrows suddenly at its distal end on joining the vas deferens; and the penis appendix is twice as long as the epiphallus and terminates in a well-differentiated bulb. In Group 2, only No. 20 agrees exactly with this description, and none of the characters mentioned is constant.

According to HUDEC (1960), the transition from the epiphallus to the vas deferens, gradual in *Cochlicopa lubricella* and abrupt in *C. lubrica*, is one of the genital characteristics best differentiating the two species. In the specimens we examined, this character exhibited a range of intermediate forms, with classification as gradual or abrupt being subjective in some cases. As with Group 2, above, this variability is not explained solely by the locality and recollection date of examined specimens (Table 5).
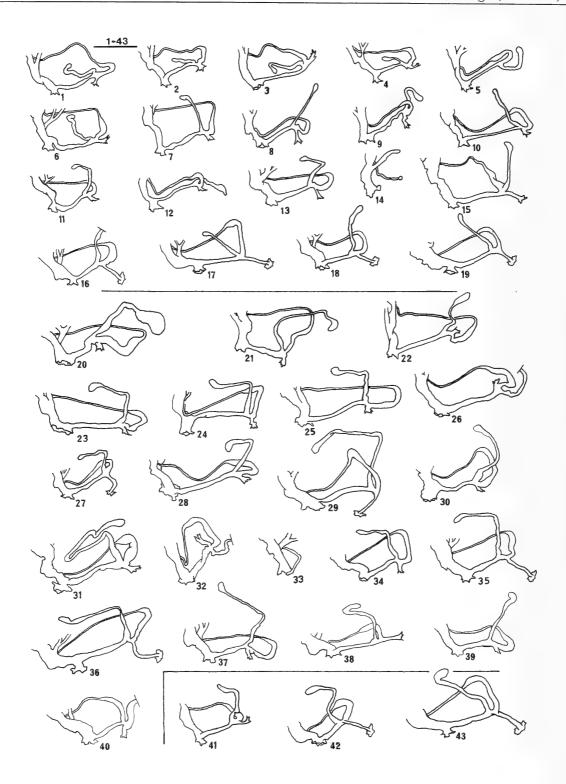
In Group 3, the male genitalia of No. 41 agree with the description of *Cochlicopa lubricella*, while those of Nos. 42 and 43 are closer to the description of *C. lubrica*.

Male genitalia were lacking in Nos. 14 and 33.

Table 5

Date (day-month-year), locality of collection, and measurements (in mm) of the characters with taxonomic value of examined specimens. Numeration as in Figure 4: Nos. 1–19, Group 1; Nos. 20–40, Group 2; Nos. 41–43, Group 3; further explanation in the text. Loc.: locality; D: diameter; H: height; P: penis; EP: epiphalus; PA: penial appendix. Abbreviations as in Table 1.

No.	Date	Loc.	D	H	P	EP	PA	No.	Date	Loc.	D	H	P	EP	PA
1	24-IX-83	HO	1.86	4.37	1.13	0.75	1.16	22	24-IX-83	LM	2.65	6.47	1.45	0.90	1.53
2			1.89	4.55	0.81	0.67	0.54	23	19-XII-83		2.47	5.19	1.38	1.18	1.84
3			1.92	4.38	1.38	0.75	1.10	24			2.80	5.80	1.50	1.23	1.75
4			1.96	4.71	0.75	0.75	—	25	05-III-84		2.62	5.54	1.63	1.06	1.62
5			2.00	4.65	1.06	0.87	1.00	26			2.62	6.12	1.50	1.13	—
6			2.02	4.90	1.17	0.63	1.13	27	19-XII-83	RB	2.60	5.69	0.95	0.87	1.37
7			2.03	4.65	1.09	0.68	1.13	28			2.62	5.85	1.63	1.17	1.80
8			2.03	4.91	0.91	0.62	1.21	29			2.67	5.86	1.63	1.44	3.54
9			2.25	5.03	1.18	0.75	1.13	30			2.69	6.02	1.06	1.29	2.13
10			2.34	5.88	1.50	0.94	1.20	31			2.89	6.15	1.50	1.06	4.06
11	19-XII-83	RB	2.05	5.16	0.88	0.80	1.21	32	06-III-84		2.84	6.47	0.88	1.25	—
12	06-III-84		2.08	4.81	1.21	0.56	1.00	33	18-XII-83	SM	2.47	5.40	—	—	—
13	19-XII-83		2.23	5.10	1.06	0.81	1.37	34	06-III-84		2.49	5.14	0.98	1.09	1.65
14			2.23	5.36	—	—	—	35	18-XII-83		2.49	5.45	1.04	0.83	2.18
15	06-III-84	SM	2.10	5.20	1.28	0.72	1.28	36	06-III-84		.2.54	5.37	1.50	1.06	2.41
16	18-XII-83		2.10	4.59	0.88	0.68	—	37			2.55	5.27	0.88	1.12	2.36
17			2.11	4.83	1.13	1.23	1.21	38	18-XII-83		2.55	5.45	1.25	0.75	1.69
18			2.12	4.73	0.88	0.75	1.34	39			2.59	5.79	0.84	0.84	1.50
19			2.19	4.99	1.16	0.77	1.25	40			2.74	6.29	0.90	0.95	—
20	24-IX-83	LM	2.39	5.49	0.78	1.29	2.63	41			2.33	5.59	0.92	0.77	1.50
21			2.60	5.41	0.94	1.06	2.69	42			2.33	5.73	0.75	0.84	1.75
								43			2.35	5.99	1.28	1.34	2.13

Figure 4

The male genitalia of the specimens examined. Scale, 1 mm.

DISCUSSION

Numerous authors have reported the existence of forms intermediate between *Cochlicopa lubricella* and *C. lubrica* (ADAM, 1960; WALDÉN, 1965; PAUL, 1975; KERNEY & CAMERON, 1979; GITTENBERGER, 1983). QUICK (1954) himself recognized the existence of specimens that could not be determined with certainty, and in agreement with our findings reported overlap between the shell diameters of the two species at around 2.3 mm.

PAUL (1975), WALDÉN (1965), and GITTENBERGER *et al.* (1970) mentioned the possibility that *Cochlicopa repentina* Hudec, 1960, might be present in Europe. The shell of this species is similar to that of *C. lubrica,* with the difference being that the peristome is whitish, and shines through with ochre color on the inner side. Its genitalia, however, are more similar to those of *C. lubricella,* except that the male part is bigger in proportion, the penis appendix is rather longer than the epiphallus, and the bulb of the penis appendix is somewhat more developed; as in *C. lubricella,* the transition from epiphallus to vas deferens is gradual (HUDEC, 1960). Of the specimens we examined, those best fitting this description are Nos. 27, 34, 38 and 39, all of which have shells similar to that of *C. lubrica* and genitalia similar to those of *C. lubricella.* However, in No. 38 the transition from epiphallus to vas deferens is abrupt; and of the others, only No. 39 has a shell with a whitish inner peristome edge. It therefore seems likely that the resemblance of these specimens to *C. repentina* is due to the variability of the characters, not to the presence of this species in O Courel.

Our findings show that none of the characters differentiating *Cochlicopa lubricella* from *C. lubrica* allow definite identification of all our specimens. The shells overlapped in maximum diameter, height, and height-diameter ratio; there were no significant differences between the height-diameter correlations of the two species; morphological characters exhibited gradients, assignment to one or other type being very subjective in some cases; and the anatomy and relative dimensions of genital structures were variable, with few specimens agreeing fully with the descriptions given by QUICK (1954) and HUDEC (1960). Furthermore, the shells of the high broom scrub population differed both from those of the other populations studied and from the descriptions of the two species.

The great variability of the "differential" characteristics and the presence of intermediate forms make it questionable whether *Cochlicopa lubricella* and *C. lubrica* should be considered as two distinct species. Some of the shell data nevertheless support their being distinguished: in the mixed populations, specimens with shell diameters in the range where the two species overlap are relatively rare (just 12.3%), and since the diameters and heights of shells in these populations are far from being normally distributed, specimens might well be extreme forms of one or other of the species rather than hybrids; this hypothesis is supported by GITTENBERGER's (1983) reporting the existence of mixed populations with no intermediate forms.

In conclusion, the status of *Cochlicopa lubrica* and *C. lubricella* remains doubtful. In our opinion, in the absence of conclusive evidence, they should not be considered as separate species. As QUICK (1954) has pointed out, breeding experiments in captivity are necessary in order to find out whether fertile hybrids are produced.

Alternatively, their enzymatic polymorphism should be investigated. Should such decisive studies show both species to be valid, new taxonomic characteristics would have to be sought in order to allow reliable identification of specimens that cannot at present be classed as one or the other.

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NOTES, INFORMATION & NEWS

Tattoo Ink as a Tag
for Nudibranchs
by
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Moss Landing, California 95039, USA

This paper describes a simple, inexpensive tagging method created for monitoring individual nudibranchs in the field. The objective was to determine if various non-toxic dyes injected into the dorsum of *Doriopsilla albopunctata* (Cooper, 1863) provide a viable method of tagging and tracking these and other nudibranch species. Previous methods used to mark shell-less mollusks have included dabbing vital stains onto a scraped area of the dorsum (ANDERSON, 1973), without positive results, and injection of pulmonate slugs using a Panjet Inoculator (HOGAN & STEELE, 1986). This latter method was successful but expensive.

Using a disposable 1-cc tuberculin syringe with a No. 25 needle (15-mm long), the injection technique was practiced on the skin of a lemon, which looks and feels remarkably similar to *Doriopsilla albopunctata*. Red food coloring (Schilling) was used to test the method of injection. Having practiced the technique, the longevity of marks was tested on nudibranchs.

Collected animals were allowed to acclimate to their aquarium situation before being injected. Using a method described by KELLY (1967) for fish, the best marks on the nudibranch were obtained. This involves inserting the tip of the needle posteriorly on the dorsum, and running the tip just under the skin horizontally so it is still visible. Then, as the needle is withdrawn, a gentle pressure is placed on the plunger to leave a distinct line of dye. Syringes could be reused if rinsed in alcohol.

All injections were done in a laboratory situation to observe whether the animals were physically affected by the mark and to observe the longevity of the tags. All animals were maintained in small floating plastic and mesh containers. To ensure that these injections could be used effectively on any size nudibranch, without causing excessive trauma, animals ranging in size from 1.5 to 3 cm were injected.

Some specimens of *Doriopsilla albopunctata* were injected with red or blue food coloring, but these marks faded rapidly. The vital stain Janus Green B C.I. No. 11050 (LILLIE, 1969) was then tried. This stain is considered to be more resistant to fading than Methylene Blue (CONN *et al.* 1962), which had been used by ANDERSON (1973). This stain lasted less than four days.

Finally, a group of animals were injected with black roll-on tatto ink, diluted just enough to make it easier to draw into the syringe. Animals were measured and injected in various areas with 1–3 marks of ink. The clearest marks were obtained when the animal was injected as shallow as possible in the dorsum. Four animals were left untagged as controls for possible toxicity of ink. The tagged slugs retained their marks for six weeks, prior to release after completion of the project, and I suspect that these marks will remain visible throughout the animal's lifetime. The tags are obvious and could not be mistaken for natural markings.

Doriopsilla albopunctata did not appear to be excessively traumatized by the injection technique. Upon puncture of the skin, they would contract and secrete mucus, but as soon as the needle was withdrawn, they relaxed and crawled around in a normal manner. Smaller animals were not affected any more than large ones.

The only fatalities sustained in these experiments were two tattooed and two untagged animals. These fatalities were probably due to the death of the sponge prey, which had begun to rot in the containers, creating a film that decreased water flow. I believe lack of oxygen was the cause of death rather than ink poisoning since the survivors appeared to be unaffected. No significant changes were seen in the size of any of the surviving animals from the beginning to the end of the experiment.

This tagging method worked best using tattoo ink injected just below the skin in a discrete line on the dorsum. By applying the ink in various colors and locations on the dorsum, many dimensions can be added to individual tagging possibilities for relocation in the field. The ink is non-toxic to the animals and is long lasting. The next step is to see how long tags last under field conditions. Nudibranchs have a short life-span, which makes their study difficult in the field. Tagging would allow tracking of an individual during its lifetime after settlement.

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Information for Contributors

Manuscripts

Manuscripts must be typed on white paper, 8½" by 11", and double-spaced throughout (including references, figure legends, footnotes, and tables). If computer generated copy is to be submitted, margins should be ragged right (*i.e., not* justified). To facilitate the review process, manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics. Metric and Celsius units are to be used.

The sequence of manuscript components should be as follows in most cases: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, figures, footnotes, and tables. The title page should be on a separate sheet and should include the title, author's name, and address. The abstract should describe in the briefest possible way (normally less than 200 words) the scope, main results, and conclusions of the paper.

Literature cited

References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Smith, 1951), for two authors (Smith & Jones, 1952), and for more than two (Smith *et al.,* 1953).

The "literature cited" section must include all (but not additional) references quoted in the text. References should be listed in alphabetical order and typed on sheets separate from the text. Each citation must be complete, with all journal titles *unabbreviated,* and in the following form:

a) Periodicals

Cate, J. M. 1962. On the identifications of five Pacific *Mitra.* The Veliger 4:132–134.

b) Books

Yonge, C. M. & T. E. Thompson. 1976. Living marine molluscs. Collins: London. 288 pp.

c) Composite works

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117–135. *In:* R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal Invertebrates of California. Stanford Univ. Press: Stanford, Calif.

Tables

Tables must be numbered and each typed on a separate sheet. Each table should be headed by a brief legend.

Figures and plates

Figures must be carefully prepared and should be submitted ready for publication. Each should have a short legend, listed on a sheet following the literature cited.

Text figures should be in black ink and completely lettered. Keep in mind page format and column size when designing figures.

Photographs for half-tone plates must be of good quality. They should be trimmed off squarely, arranged into plates, and mounted on suitable drawing board. Where necessary, a scale should be put on the actual figure. Preferably, photographs should be in the desired final size.

It is the author's responsibility that lettering is legible after final reduction (if any) and that lettering size is appropriate to the figure. Charges will be made for necessary alterations.

Processing of manuscripts

Upon receipt each manuscript is critically evaluated by at least two referees. Based on these evaluations the editor decides on acceptance or rejection. Acceptable manuscripts are returned to the author for consideration of comments and criticisms, and a finalized manuscript is sent to press. The author will receive from the printer two sets of proofs, which should be corrected carefully for printing errors. At this stage, stylistic changes are no longer appropriate, and changes other than the correction of printing errors will be charged to the author at cost. One set of corrected proofs should be returned to the editor.

An order form for the purchase of reprints will accompany proofs. If reprints are desired, they are to be ordered directly from the printer.

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